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TEMPORAL, SPATIAL, AND ENVIRONMENTAL INFLUENCES ON THE DEMOGRAPHICS OF GRIZZLY BEARS IN THE GREATER YELLOWSTONE ECOSYSTEM

CHARLES C. SCHWARTZ
U.S. Geological Survey, Northern Rocky Mountain Science Center, Interagency Grizzly Bear Study Team, Forestry Sciences Lab, Montana State University, Bozeman, MT 59717, USA
MARK A. HAROLDSON
U.S. Geological Survey, Northern Rocky Mountain Science Center, Interagency Grizzly Bear Study Team, Forestry Sciences Lab, Montana State University, Bozeman, MT 59717, USA
GARY C. WHITE
Department of Fishery and Wildlife Biology, Colorado State University, Fort Collins, CO 80523, USA
RICHARD B. HARRIS
Wildlife Biology Program, College of Forestry and Conservation, University of Montana, Missoula, MT 59812, USA
STEVE CHERRY
Department of Mathematical Sciences, Montana State University, Bozeman, MT 59717, USA
KIM A. KEATING
U.S. Geological Survey, Northern Rocky Mountain Science Center, Forestry Sciences Lab, Montana State University, Bozeman, MT 59717, USA
DAVE MOODY
Trophy Game Section, Wyoming Game and Fish Department, 260 Buena Vista, Lander, WY 82520, USA
CHRISTOPHER SERVHEEN
U.S. Fish and Wildlife Service, University of Montana, Missoula, MT 59812, USA

Abstract: During the past 2 decades, the grizzly bear (*Ursus arctos*) population in the Greater Yellowstone Ecosystem (GYE) has increased in numbers and expanded in range. Understanding temporal, environmental, and spatial variables responsible for this change is useful in evaluating what likely influenced grizzly bear demographics in the GYE and where future management efforts might benefit conservation and management. We used recent data from radiomarked bears to estimate reproduction (1983–2002) and survival (1983–2001); these we combined into models to evaluate demographic vigor (lambda [λ]). We explored the influence of an array of individual, temporal, and spatial covariates on demographic vigor.

We identified an important relationship between λ and where a bear resides within the GYE. This potential for a source–sink dynamic in the GYE, coupled with concerns for managing sustainable mortality, reshaped our thinking about how management agencies might approach long-term conservation of the species. Consequently, we assessed the current spatial dynamic of the GYE grizzly bear population. Throughout, we followed the information-theoretic approach. We developed suites of a priori models that included individual, temporal, and spatial covariates that potentially affected

reproduction and survival. We selected our best approximating models using Akaike's information criterion (AIC) adjusted for small sample sizes and over-dispersion (AIC$_c$ or QAIC$_c$, respectively).

We provide recent estimates for reproductive parameters of grizzly bears based on 108 adult (>3 years old) females observed for 329 bear-years. We documented production of 104 litters with cub counts for 102 litters. Mean age of females producing their first litter was 5.81 years and ranged from 4 to 7 years. Proportion of nulliparous females that produced cubs at age 4 to 7 years was 9.8, 29.4, 56.4, and 100%, respectively. Mean (± SE) litter size (n = 102) was 2.0 ± 0.1. The proportion of litters of 1, 2, and 3 cubs was 0.18, 0.61, and 0.22, respectively. Mean yearling litter size (n = 57) was 2.0 ± 0.1. The proportion of litters containing 1, 2, 3, and 4 yearlings was 0.26, 0.51, 0.21, and 0.02, respectively. The proportion of radiomarked females accompanied by cubs varied among years from 0.05 to 0.60; the mean was 0.316 ± 0.03. Reproductive rate was estimated as 0.318 female cubs/female/year. We evaluated the probability of producing a litter of 0–3 cubs relative to a suite of individual and temporal covariates using multinomial logistic regression. Our best models indicated that reproductive output, measured as cubs per litter, was most strongly influenced by indices of population size and whitebark pine (*Pinus albicaulis*) cone production. Our data suggest a possible density-dependent response in reproductive output, although perinatal mortality could have accounted for the correlation.

We analyzed survival of cubs and yearlings using radiotelemetry of 49 unique female bears observed with 65 litters containing 137 dependent young. We documented 42 deaths: 32 cubs, 5 yearlings, and 5 that could have died as a cub or yearling. Using a nest survival estimator coded in Program MARK, our best model indicated cub and yearling survival were most affected by residency in the GYE. Survival was highest for cubs and yearlings living outside Yellowstone National Park (YNP) but within the U.S. Fish and Wildlife Service (USFWS) Grizzly Bear Recovery Zone (RZ). Cubs and yearlings living inside YNP had lower survival and those living outside the RZ had the lowest survival rates. Survival rates were negatively related to a population index, suggesting density-dependence. Survival improved with: higher whitebark pine seed production, greater winter severity, larger litter size, and higher female (mother's) age. We tested theories of sexually selective infanticide, but results were equivocal.

We investigated factors influencing survival of subadult and adult grizzly bears using data from 323 radio-instrumented bears monitored for 5,989 months. Telemetry records were converted into monthly encounter histories, and survival was estimated using known fate data in Program MARK. Bears were grouped into a study sample and conflict (bears specifically trapped due to conflict with humans) sample according to circumstance of capture and monitoring, with data from both contributing to survival estimates. A censored (*C*) data set included 69 documented mortalities but censored 22 bears with unknown fate. A second, assumed dead (*AD*) data set, considered these 22 bears as mortalities.

Most known mortalities (85.5%) were human-caused, with 26 and 43 from the study and conflict samples, respectively. Mean annual survival ($\bar{S}_F$) for study sample female bears using *C* and *AD* data sets were $\bar{S}_{C\,F}$ = 0.950 (95% CI = 0.898–0.976) and $\bar{S}_{AD\,F}$ = 0.922 (95% CI = 0.857–0.995). Process standard deviation (SD) for study

sample females bears was estimated at $SD_C = 0.013$ and $SD_{AD} = 0.034$. Our best models indicated study sample bears survived better than conflict sample bears, females survived better than males, survival was lowest during autumn, and survival increased during years with good whitebark pine cone production. Bears with a higher proportion of annual locations outside the RZ exhibited poorer survival than individuals located more frequently inside YNP, the RZ, or both. Indices of winter severity, ungulate biomass, and population size, plus individual covariates including presence of dependent young, prior conflicts with humans, and age class were not important predictors of survival in our models. We documented a trend of increased survival through the study that was offset in recent years by lower survival of bears located more frequently outside the RZ. This result suggests that efforts to reduce female mortality initiated in 1983 were successful, and similar measures outside the RZ would improve the prospect for continued growth and expansion of the GYE grizzly bear population.

To estimate sustainable mortality of the population, we produced trajectories of the GYE grizzly bear population under a range of survival rates of independent females (>2 years old) using an individual-based, stochastic simulation program and demographic data from radiomarked bears. We incorporated yearly (process) variation in survival rates, as estimated from data after removing sampling variation. We summarized trajectories by mean λ and by probability of $\lambda < 1$, both within a 10-year period, and examined sensitivity of results by altering our initial assumptions to reflect uncertainty. Because process variation of female survival was low, λ decreased stochastically only slightly from that expected under a completely deterministic model. Uncertainty about mean cub and yearling survival rates was considerable, but because λ was relatively insensitive to these parameters, incorporating this uncertainty also lowered resulting trajectories only slightly. Uncertainty about independent female survival had a much larger effect on probability of population decline despite having little effect on expected λ. Under our current understanding of the GYE grizzly bear population dynamics, λ was independent of male survival rate; variation in male mortality produced only short-term effects on abundance and long-term effects on sex ratio. The appropriate mortality target for independent female bears depends on the risk of a population decline (i.e., $\lambda < 1$) that managers and the public are willing to accept. For the chance of a population decline to be $\leq 5\%$ under conditions applying during 1983–2002, annual mortality of independent females would have to be $\leq 10\%$. Projections are useful only if viewed over a relatively short time frame because they were based solely on mean 1983–2002 conditions and because small samples make it difficult for managers to know the true mortality rate.

To further explore the implications of geographic structure in female survival, we built an array of deterministic models using estimates of reproduction and survival from our best models. We calculated deterministic estimates of λ incorporating our residency covariate plus changes in whitebark pine cone production and winter severity. A source–sink dynamic is suggested for the GYE, with $\lambda \geq 1$ inside YNP and the RZ but $\lambda \leq 1$ outside the RZ. Such a source–sink dynamic requires new discussions about population management, mortality thresholds, and elimination of anthropogenic foods on the edge of the ecosystem. To enhance future management, we present food and population monitoring guidelines that should be considered in light of our findings.

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Key words: Akaike's information criterion, demography, density dependence, Greater Yellowstone Ecosystem, grizzly bear, population regulation, precautionary principle, reproduction, sexually selective infanticide, source–sink dynamics, survival, *Ursus arctos*

Las influencias temporales, espaciales, y ambientales en los demogáficos del oso pardo del Ecosistema Mayor de Yellowstone

Resumen: Durante las dos últimás décadas, la población del oso pardo (*Ursus arctos*) ha aumentado en números y se ha extendido geograficamente. Es útil entender los variables temporales, ambientales y espaciales que provocan este cambio, primero para evaluar las probables influencias sobre los demográficos del oso pardo en *The Greater Yellowstone Ecosystem* (el ecosistema mayor de Yellowstone) (GYE), y segundo para saber dónde dedicar los futuros esfuerzos que puedan beneficiar la conservación y el manejo de la población. Hemos utilizado datos de osos radiomarcados para medir y evaluar la reproducción (1983–2002) y la supervivencia (1983–2001). Hemos combinado estos datos y los hemos puesto en modelos para evaluar el vigor demográfico (lambda [λ]). Hemos explorado la influencia de una serie de covariables individuales, temporales, y espaciales sobre el vigor demográfico.

Hemos identificado una relación importante entre λ y el lugar donde reside el oso dentro del GYE. La existencia potencial de una dinámica fuente-sumidero junto a la necesidad de manejar una tasa sostenible de mortalidad, nos llevaron a replantear la cuestión acerca de que cómo las agencias administrativas pueden abordar la conservación a largo plazo de la especie. Por consiguiente, hemos evaluado al actual dinámica espacial de la población del oso pardo del GYE. A lo largo de nuestra investigación hemos seguido el plantamiento de información teórica, desarrollando grupos de modelos "*a priori*" que incluyeron covariables individuales, temporales, y espaciales que posiblemente afectan la reproducción y la supervivencia. Escogimos nuestros mejores modelos aproximantes usando *Akaike's information criteria* (*AIC*) (los criterios de información de Akaike) ajustados para muestras de un tamaño pequeño y la sobredispersión (AIC_c y $QAIC_c$, respectivamente).

Hemos proporcionado estimaciones recientes para los parámetros reproductivos del oso pardo basadas en 108 hembras adultas (>3 años de edad) observadas durante 329 años cumulativos**.** Hemos documentado la producción de 104 camadas y hemos hecho un recuento de oseznos de 102 camadas. El promedio de edad de las hembras (madres) produciendo una primera camada fue 5.81 años y variaba desde los 4 años hasta los 7 años. La proporción de hembras nuliparas que produjeron oseznos a las edades de 4, 5, 6, y 7 años fue 9.8, 29.4, 56.4, y 100%, respectivamente. El promedio del tamaño (± *SE*) de camadas ($n = 102$) fue 2.0 ± 0.1. La proporción de las camadas de 1, 2, y 3 oseznos fue 0.18, 0.61, y 0.22, respectivamente. El promedio del tamaño de camadas anuales ($n = 57$) fue 2.0 ± 0.1. La proporción de camadas que contenían 1, 2, 3, y 4 oseznos anuales fue 0.263, 0.51, 0.21, y 0.02, respectivamente. La proporción de hembras radiomarcadas acompañadas de oseznos varió a través de los años desde 0.05 hasta 0.60; el promedio fue 0.316 ± 0.03. La tasa reproductiva se estimó en 0.318 oseznos/hembra/año. Hemos usado una regresión logística multivariable para evaluar la probabilidad de que las hembras produjeran una camada de 0 a 3 oseznos relativo a un conjunto de covariables individuales y temporales. Nuestros mejores modelos indicaron que el rendimiento

reproductor**,** medido según el número de oseznos por camada, fue influido sobre todo por los índices del tamaño de la población, y la producción de conos del pino *whitebark* (*Pinus albicaulis*). Nuestros datos sugieren que el rendimiento reproductor depende de la densidad de la población aunque la mortalidad perinatal podría haber sido también la causa de la correlación.

Hemos analizado la supervivencia de oseznos y de oseznos anuales usando radiotelemetría de 49 hembras distintas observadas con 65 camadas de 137 crías dependientes. Documentamos 42 muertes: 32 oseznos, 5 oseznos anuales y 5 que murieron bien como osezno o bien como osezno anual. Usando una fórmula que calcula la supervivencia del nido, encodado en el programa *MARK*, nuestro mejor modelo indicó que la supervivencia de los oseznos y oseznos anuales, había sido afectada principalmente por la residencia en el *GYE*. La supervivencia fue más alta para oseznos y oseznos anuales que vivían fuera de El Parque Nacional de Yellowstone (*YNP*) pero dentro de la zona recuperatoria del oso pardo (*Grizzly Bear Recovery Zone)* (*RZ*) del *US Fish and Wildlife Service* (*USFWS*). Oseznos y oseznos anuales que vivían dentro del *YNP* tenían tasas de supervivencia más bajas mientras que los que vivían fuera de la zona recuperatoria tuvieron las tasas incluso más bajas. Las tasas de supervivencia se relacionaron negativamente con un índice de población, lo cual sugiere que las tasas dependen de la densidad de población. La supervivencia mejoró con los siguientes fenómenos: una producción más alta de semillas del pino *whitebark*, una mayor severidad del invierno, un tamaño más grande de camada y una edad avanzada de la hembra (madre). Probamos teorías referentes al infanticidio (seleccionado por género), pero los resultados fueron equívocos.

Hemos investigado los factores que influían la supervivencia de osos pardos subadultos y adultos usando los datos de 323 osos radioinstrumentados, seguidos durante 5,989 meses cumulativos. Se convirtieron en registros de telemetría en historiales de encuentros mensuales, y se estimó la supervivencia según los datos de aquellos osos con destinos conocidos en el Programa *MARK.* Los osos fueron agrupados en una muestra de estudio y en otra de conflicto (que fueron osos que habían sido atrapados debido a un conflicto con los humanos) según las circunstancias de captura y seguimiento. Los datos que sacamos de ambos grupos contribuyeron a las estimaciones de supervivencia. Una serie de datos censurados (*C*) incluía 69 mortalidades documentadas pero censuró 22 osos con destinos desconocidos. Una segunda serie de datos de osos cuyas muertes dimos por sentado (*AD*), consideró estos 22 osos como mortalidades.

La mayoría de las mortalidades conocidas (85.5%) fue causada por humanos con 26 mortalidades de la muestra de estudio y 43 de la muestra de conflicto. El promedio de la supervivencia anual para hembras de la muestra de estudio ($\bar{S}_{C\,F}$), usando las series de datos C y AD fue $\bar{S}_{C\,F}$ = 0.950 (95% CI = 0.898–0.976) y $\bar{S}_{AD\,F}$ = 0.922 (95% CI = 0.857–0.995). La desviación estandar de proceso (SD) para la muestra de hembras se estimó en $SD_C = 0.013$ y $SD_{AD} = 0.034$. Nuestros mejores modelos indicaron que los osos de la muestra de estudio sobrevivieron mejor que los osos de la muestra de conflicto; las hembras sobrevivieron mejor que los machos; la supervivencia fue más baja durante el otoño; y la supervivencia aumentó durante los años con una buena producción de conos del pino *whitebark* (*Pinus albicaulis*). Los osos con un porcentaje más alto de ubicaciones (que habían sido localizados a través de tomas radiotransmitidas) fuera de la

RZ mostraron tasas de menos supervivencia que aquellos que fueron localizados con más frecuencia dentro de o *YNP*, o *RZ*, o los dos. Los índices de la severidad del invierno, la biomasa ungulada, y el tamaño de la población, además de los covariables individuales, (que incluyeron la presencia de crías dependientes, conflictos anteriores con humanos, y edad), no fueron pronósticos importantes de la supervivencia en nuestros modelos. A través del estudio, hemos documentado una tendencia de supervivencia aumentada en años recientes contrapesada con una tasa más baja de osos que se ubicaron frecuentamente fuera de la *RZ*. Este resultado sugiere que los esfuerzos que se iniciaron en 1983 para reducir la mortalidad femenina, tuvieron éxito y también sugiere que las medidas semejantes aplicadas fuera de la *RZ* mejorarían las expectativas de la aumentación y expansión de la población del oso pardo del *GYE*.

Con el fin de calcular la mortalidad sostenible de la población determinamos trayectorias de la población del oso pardo del *GYE* a través de una escala de tasas de supervivencia de hembras independientes (>2 años de edad). Para determinar estas trayectorias utilizamos un programa de simulación estocástica, basado en osos individuales y datos demográficos de osos radiomarcados. Incorporamos la variación anual de proceso en las tasas de supervivencia, tal como fueron estimados de los datos después de haber eliminado la variación derivida de las muestras. Resumimos las trayectorias usando el promedio de λ y la probabilidad de que $\lambda < 1$, (los dos dentro de un período de diez años). También examinamos la vulnerabilidad de los resultados alterando nuestras suposiciones iniciales para reflejar incertidumbre. Dado que la variación de proceso de la supervivencia femenina fue baja, λ disminuyó estocasticamente solamente un poco de lo que habríamos esperado usando un modelo completemente determinístico. La incertidumbre alrededor de las tasas de supervivencia de oseznos y oseznos anuales fue considerable. Sin embargo, ya que λ fue relativamente invulnerable a estos parámetros, la incorporación de esta incertidumbre también bajó minimamente las trayectorias resultantes. La incertidumbre alrededor de las tasas de supervivencia de hembras independientes tuvo un efecto mucho más grande sobre la probabilidad de un descenso de la población a pesar de no tener mucho efecto sobre λ esperado. Según nuestro entendimiento actual sobre las dinámicas de población del oso pardo, λ fue independiente de la tasa de supervivencia de los machos; la variación de la mortalidad de machos produjo solamente efectos de corto plazo sobre la abundancia y efectos de largo plazo sobre la relación de género. La meta razonable de mortalidad para hembras independientes depende de hasta qué punto los administadores y el público estén dispuestos a arriesgar un descenso de la población (i.e., $\lambda < 1$). Con el fin de que la posibilidad de un descenso de población sea $\leq 5\%$, bajo las condiciones existentes durante 1983–2002, la mortalidad anual tendría que ser $\leq 10\%$. Las proyecciones son útiles sólo si son observadas durante un período relativamente corto ya que fueron basadas solamente en el promedio de las condiciones de 1983–2002 y ya que las muestras pequeñas ponen dificultades a los administradores para saber la tasa verdadera de la mortalidad.

Para continuar explorando las implicaciones de la estructura geográfica en la supervivencia de las hembras, construímos una serie de modelos determinísticos usando estimaciones de reproducción y supervivencia derivadas de nuestros mejores modelos. Realizamos estimaciones determinísticas de λ incorporando nuestro covariable de residencia, y también los cambios en la producción de conos del pino *whitebark* y la

severidad de invierno. Se sugiere una dinámica fuente-sumidero para *GYE* con $\lambda \geq 1$ dentro de *YNP* y *RZ* pero $\lambda \leq 1$ fuera de *RZ*. Esta dinámica fuente-sumidero requiere nuevos debates sobre el manejo de la población, los umbrales de la mortalidad y la eliminación de comida antropogénica en la frontera del ecosistema. Para mejorar el manejo futuro, presentamos directrices de comida y seguimiento de la población que deberían ser consideradas en vista de las conclusiones.

INFLUENCES TEMPORELLES, SPATIALES ET ENVIRONEMENTALES SUR LA DEMOGRAPHIE DE L'OURS GRIZZLI DANS L'ECOSYSTEME DU GRAND YELLOWSTONE

Résumé: Pendant les deux dernières décennies, la population des ours grizzlis (*Ursus arctos*) de l'écosystème du Grand Yellowstone (Greater Yellowstone Ecosystem GYE) a augmenté en nombre et s'est étendue géographiquement. Il est important de comprendre les variables temporelles, écologiques et spatiales, responsables de ce changement pour évaluer ce qui a influencé la démographie des ours grizzlis dans le GYE et où les futurs efforts de gestion seront favorables à la conservation et au maintien des ours. Nous avons utilisé des données récentes recueillies à partir de colliers-radio télémétriques dont les ours sont munis, pour faire une estimation de leur reproduction (1983–2002) et de leur survie (1983–2001); nous avons combiné ces données en modèles pour évaluer leur vigueur démographique (lambda [λ]). Nous avons dressé un ensemble de covariables individuelles, temporelles et spatiales et remarqué l'influence qu'elles avaient sur leur vigueur démographique.

Nous avons remarqué une relation importante entre λ et le lieu où l'ours réside dans le GYE. Ce potentiel de dynamique source-puits dans le GYE, associé à notre souci de gérer un taux soutenable de mortalité des ours ont changé notre façon de penser à l'approche sur laquelle les agences de gestion peuvent compter pour conserver cette espèce à long terme. Par conséquent, nous avons évalué la dynamique spatiale actuelle de la population des ours grizzlis du GYE. Tout au long de notre étude, nous avons suivi l'approche d'information théorique. Nous avons développé des suites de modèles à priori qui comprennent les covariables individuelles, temporelles et spatiales pouvant affecter la reproduction et la survie des ours. Nous avons sélectionné les meilleurs modèles approximatifs en utilisant le critère d'information Akaike (AIC), adapté à des échantillons de petites tailles et à une distribution régulière (AIC_c or $QAIC_c$, respectivement).

Nous avons fourni des estimations récentes concernant les paramètres reproductifs des ours grizzlis faites sur 108 femelles adultes âgées de plus de trois ans (> à 3 ans) observées sur 329 années de suivi d'ours. Nous avons répertorié la production de 104 portées avec un nombre d'oursons pour 102 portées. La moyenne d'âge des mères ayant eu leur première portée était de 5.81 ans et allait de 4 à 7 ans. La proportion de femelles nullipares qui ont mis bas des oursons à l'âge de 4, 5, 6 et 7 ans était de 9.8, 29.4, 56.4 et 100%. La moyenne (±SE) de la taille de la portée ($n = 102$) était de 2.0 ± 0.1. La proportion des portées de 1, 2 et 3 oursons était de 0.18, 0.61 et 0.22 respectivement. La moyenne de la taille des portées d'oursons de 1 an ($n = 57$) était de 2.0 ± 0.1. La proportion des portées ayant 1, 2, 3 et 4 petits de 1 an était de 0.263, 0.51, 0.21, et 0.02. La proportion des femelles munies de collier-radio et étant accompagnées

de leurs oursons variait de 0.05 à 0.60; la moyenne était de 0.316 ± 0.03. Le taux de reproduction a été estimé à 0.318 ourson femelle/ par femelle/par an. Nous avons évalué la probabilité de mise bas d'une portée de 0 à 3 oursons par rapport à une série de covariables individuelles et temporelles en utilisant une régression logistique multivariée. Nos meilleurs modèles ont indiqué que le rendement de reproduction, mesuré par le nombre d'oursons par portée a été fortement influencé par des indices dans la taille de la population et la production de pommes de pin du pin à écorce blanche (*Pinus albicaulis*). Nos données suggèrent une réponse possible de dépendance à la densité dans le rendement reproductif, bien que la mortalité périnatale puisse jouer un rôle dans cette corrélation.

Nous avons analysé la survie des oursons et des oursons âgés de 1 an par radiotélémétrie sur 49 femelles et leurs 65 portées avec 137 oursons dépendants (de leur mère). Nous avons compté 42 morts: 32 oursons, 5 petits de 1 an et 5 qui auraient pu mourir soit en bas âge, soit à l'âge de 1 an. En utilisant un estimateur de survie dans les nids codé dans le Programme MARK, notre meilleur modèle a indiqué que la survie des oursons et des oursons de 1 an était le plus affecté lorsqu'ils vivaient dans le GYE. Le taux de survie était plus élevé parmi les oursons et ceux âgés de 1 an vivant à l'extérieur du Parc National du Yellowstone (YNP) mais dans la zone du *service étasunien de vie aquatique et vie sauvage* (U.S Fish and Wildlife Service (USFWS) et de *la zone de récupération des ours grizzlis* (Grizzli Bear Recovery Zone (RZ). Les oursons et les oursons âgés de 1 an vivant à l'intérieur du YNP avait un taux de survie plus bas et ceux vivant à l'extérieur de RZ avaient le taux de survie le plus faible. Les taux de survie étaient négativement apparentés à un index de la population, ce qui suggère une dépendance à la densité. La survie des oursons s'est améliorée grâce à une production plus élevée de graines du pin à écorce blanche, à des hivers plus rudes, à des portées plus larges et à des femelles mères plus âgées. Nous avons testé les théories d'infanticide séléctif lié à la sexualité, mais les résultats étaient ambigus.

Nous avons cherché les facteurs influençant la survie des jeunes ours et des ours adultes en utilisant les données de 323 ours équipés de collier-radio et surveillés pendant 5,989 mois de suivi d'ours. Les enregistrements de télémétrie ont été convertis en résumés mensuels de contacts et leur survie a été évaluée à partir de cas de mortalité connus, issus du progamme Mark. Les ours ont été regroupés et étudiés à partir d'un échantillon d'étude et d'un échantillon propre au conflit (spécialement les ours capturés suite à leur conflit/contact à l'homme) compte tenu des circonstances de capture et de surveillance, avec les données des deux échantillons qui ont contribué à déterminer des estimations de survie. Un ensemble de données-censeur (C) a démontré 69 morts documentées contre 22 au sort inconnu. Un autre ensemble de données-considéré comme étant mort (assumed dead-AD) a permis de conclure que ces 22 ours étaient morts.

La plupart des cas connus de mortalité (85.5%) étaient liés à la présence humaine, avec 26 mortalités issues de l'échantillon d'étude et 43 de l'échantillon propre au conflit. La moyenne de la survie annuelle des femelles ($\overline{S}_{C\,F}$), calculée à partir de l'ensemble des données C et AD était de $\overline{S}_{C\,F}$ = 0.950 (95% CI = 0.898–0.976) and $\overline{S}_{AD\,F}$ = 0.922 (95% CI = 0.857–0.995). Le processus standard de déviation (standard deviation SD) pour l'échantillon d'étude des femelles a été estimé à SD_C = 0.013 and SD_{AD} = 0.034. Nos meilleurs modèles ont indiqué que les ours de l'échantillon d'étude survivaient mieux que les ours de l'échantillon propre au conflit, que les femelles survivaient mieux que les mâles, le taux de survie était le plus faible en automne et le taux de survie augmentait pendant les années de bonne production de pommes de pin du pin albicaule. Les ours dont la proportion de résidence annuelle à l'extérieur de RZ est plus élevée ont montré que leur taux de survie était plus faible que celui des ours vivant plus fréquemment à l'interieur du YNP ou à l'intérieur de RZ, ou des deux localités YNP et RZ. Les indices de sévérité hivernale, de biomasse ongulée et de taille de la population, avec en plus les covariables individuelles comprenant la présence de jeunes ours dépendants, les conflits/contacts précedents avec l'homme et enfin la classe d'âge n'étaient pas des éléments importants de prédiction de survie dans nos modèles. Nous avons recherché une tendance de survie accrue au travers d'une étude qui avait été contrebalancée ces dernières années par un taux de survie moins élevé chez les ours vivant plus fréquemment à l'extérieur de RZ. Ce résultat implique que les efforts, initiés en 1983, et entrepris pour réduire le taux de mortalité des femelles ont été positifs. Des mesures similaires prises à l'extérieur de RZ amélioreraient les perspectives d'avenir de l'accroissement et l'expansion de la population des ours grizzlis du GYE.

Afin d'estimer une mortalité soutenable de la population, nous avons tracé des trajectoires de la population d'ours grizzlis de GYE à partir de variations des taux de survie de femelles indépendantes (> 2ans) en utilisant un programme de simulation stochastique basé sur un individu ainsi que des données démographiques provenant d'ours munis de collier-radio. Nous y avons incorporé un processus de variation annuelle des taux de survie, tels qu'ils avaient été estimés à partir de données sans l'échantillonnage de variation. Nous avons résumé les trajectoires au moyen de λ et par la probabilité de $\lambda < 1$, sur une période de 10 ans, et avons examiné la susceptibilité des résultats en changeant nos hypothèses de départ pour qu'il y ait incertitude. Parce que le processus de variation de la survie des femelles était faible, λ a baissé stochastiquement mais très peu par rapport à ce à quoi on s'attendait avec un modèle complètement déterministe. L'incertitude quant à la moyenne des taux de survie des oursons et des oursons d'un an était considérable, mais parce que λ était relativement insensible à ces paramètres, le fait d'inclure cette incertitude n'a fait baisser que légèrement le tracé des trajectoires. L'incertitude de la survie des femelles indépendantes a eu un plus grand effet sur la probabilité du déclin de la population même si l'effet attendu sur λ était moindre. Ce que nous comprenons actuellement sur la dynamique de la population des grizzlis du GYE, c'est que λ était indépendant du taux de survie des mâles; la variation du taux de mortalité de l'ours mâle n'a produit sur l'abondance que des effets à court terme et sur le sex-ratio des effets à long terme. La cible appropriée du taux de mortalité des ourses indépendantes dépend du risque que les gestionnaires et le public veulent courir concernant le déclin de la population (par exemple, $\lambda < 1$). Pour que le déclin de la population soit ≤5% à partir des conditions appliquées depuis 1983–2002, la mortalité des femelles indépendantes devrait être ≤10%. Ces projections ne sont utiles que si elles sont observées sur une période courte parce qu'elles étaient seulement basées sur la moyenne des conditions de 1983–2002 et parce qu'il est difficile pour les gestionnaires de savoir le véritable taux de mortalité à partir de petits échantillons.

Afin d'explorer plus amplement les implications de la structure géographique dans la survie des femelles, nous avons construit un ensemble de modèles déterministes à partir d'estimations de reproduction et de survie de nos meilleurs modèles. Nous avons

calculé les estimations déterministes de λ en ajoutant la covariable de résidence et aussi les changements de production des pommes de pin du pin albicaule et la sévérité des hivers. Une dynamique source-puits est suggérée pour le GYE avec λ ≥ 1 à l'intérieur de YNP et RZ mais λ ≤ 1 à l'extérieur de RZ. Une telle dynamique source-puits suscite de nouvelles discussions au sujet de la gestion de la population, du seuil des taux de mortalité et de l'élimination d'aliments anthropogéniques que l'on trouve en bordure de l'écosystème. Pour améliorer la gestion future, nous proposons de grandes lignes concernant le *monitoring* de l'alimentation et de la population qui devraient être prises en considération compte tenu de nos résultats.

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BACKGROUND

Demographics

Caughley (1977:55) stated that "demographic vigour of a population is defined as its level of well-being in terms of fecundity and survival, as summarized by r_s." Demographic vigor reveals how well a population copes with current problems, but nothing about how a population will respond to an environmental change or how a population will persist in the future. Caughley (1977) defined demographic vigor in terms of r_s (survival–fecundity rate of increase), implied by age-specific survival and fecundity at time of measurement. Rate of increase measures a population's general well being, describing the average reaction of all members of the population to the collective action of all environmental influences. "No other statistic summarizes so concisely the demographic vigour of a population" (Caughley 1977:54). Although demographic vigor means little in a genetic or evolutionary sense, it is the fitness (i.e., state or condition) that is manipulated by management.

The history of grizzly bears in the GYE is typical for the species in the conterminous United States south of Canada. Before European colonization, grizzly bears enjoyed a wide distribution (Rausch 1963, Martinka 1976, Servheen 1999, Schwartz et al. 2003*a*). With settlement and conquest of western North America, grizzlies were eliminated from 98% of historic range during a 100-year period (Mattson et al. 1995). Of 37 grizzly populations present in 1922, 31 were extirpated by 1975 (Servheen 1999).

In 1959, when Craighead et al. (1995) began pioneering work on grizzly bears in Yellowstone, the population had been reduced to a fraction of its former size and was relegated largely to YNP and surrounding environs. High grizzly bear mortality in 1970 and 1971 following closure of open-pit dumps in YNP (National Academy of Sciences 1974) and uncertainty about population status prompted the USFWS to list the species as threatened south of Canada under the Endangered Species Act in 1975 (USFWS 1993).

Bear numbers continued to decline after listing, and early research (Knight and Eberhardt 1984) suggested that the balance between a stable population or one in decline might be determined by the fate of as few as 2 adult females (Knight and Eberhardt 1987). Such estimates were premised on a 1980 estimate of about 30 adult females in the population (Knight and Eberhardt 1984). Adult female survival was identified as the most important vital rate influencing population trend (Eberhardt 1977). Knight and Eberhardt (1985) identified low adult female survival as the critical parameter causing a decline in the GYE prior to the mid-1980s, and strategies were implemented to improve female survival (Interagency Grizzly Bear Committee 1986). Those strategies were aimed primarily at reducing human-caused bear mortality. Management actions to reduce human-caused mortality were implemented in the early 1980s (Knight et al. 1999). Since listing grizzly bears as threatened, efforts toward recovery have included preparation and multi-agency implementation of 2 versions of a Recovery Plan (USFWS 1982, 1993).

Since the grizzly bear population's nadir in the mid-1980s, evidence from a variety of sources indicates that grizzly bear numbers in the GYE have increased through the 1990s. Counts of unique females with cubs-of-the-year (i.e., unduplicated females as per Knight et al. 1995, Haroldson and Schwartz 2002) have increased and geographic distribution of grizzly bears has expanded (Basile 1982, Blanchard et al. 1992, Schwartz et al. 2002, Pyare et al. 2004). Consistent with these trends, estimates of λ derived from radiomonitored bears indicated a positive population trend (Eberhardt et al. 1994, Eberhardt 1995, Boyce et al. 2001), due in large part to reduced female mortality.

Humans have been and remain the single greatest cause of grizzly bear mortality (McLellan et al. 1999). Managing human-caused mortality has been an integral component of recovery for grizzly bears in the GYE (Knight and Eberhardt 1985, Eberhardt et al. 1986). Since adopting the federal Recovery Plan for grizzly bears in the United States (USFWS 1982, 1993), mortality has been monitored and a standard for acceptable mortality limits established. One important component of the limits of acceptable mortality is an estimate derived by Harris (1986) of maximum human-caused mortality sustainable by a grizzly bear population. This estimate of sustainable mortality was developed from a model of a generic bear population in the Rocky Mountains. Harris (1986) suggested that grizzly bear populations could sustain approximately 6% human-caused mortality without population decline. To facilitate recovery and to account for unknown, unreported human-caused mortality, known human-caused mortality was set by the USFWS Grizzly Bear Recovery Plan at 4% of the minimum population estimate (USFWS 1993).

Environmental

The GYE contains extensive populations of ungulates, primarily elk (*Cervus elaphus*) and bison (*Bison bison*), but including mule and white-tailed deer (*Odocoileus hemionus, O. virginianus*), bighorn sheep (*Ovis canadensis*), pronghorn (*Antilocapra americana*), mountain goat (*Oreamnos americanus*), and moose (*Alces alces*). Winter-killed elk and bison have been identified as important spring food to bears (Green et al. 1997, Mattson 1997*a*). Grizzly bears prey on elk calves during late May through early July (Gunther and Renkin 1990) and to a lesser extent on older classes of elk throughout the year (Mattson 1997*a*). Grizzly bears take adult moose (Mattson 1997*a*), and predation on bison has been documented (Varley and Gunther 2002, Wyman 2002). Bears opportunistically use carcasses throughout the year and, since reintroduction of grey wolves (*Canis lupus*) in 1997, usurp wolf kills (D. Smith, YNP, personal communication). Concentration of isotopic nitrogen ($\delta^{15}N$) in grizzly bear hair suggests that meat constitutes 45 and 79% of annual diets for females and males, respectively (Jacoby et al. 1999). Consumption of meat increases in years of poor whitebark pine cone production (Mattson 1997*a*, Felicetti et al. 2003).

Other important animal foods include cutthroat trout (*Oncorhynchus clarki*) and army cutworm moths (*Euxoa auxiliaris*) (Mattson et al. 1991*a*, *b*; French et al. 1994). Spawning cutthroat trout are obtained during mid-May through July from tributary streams to Yellowstone Lake (Reinhart and Mattson 1990). Summer aggregations of army cutworm moths occur on high-elevation talus slopes in the southeastern portion of the GYE and are consumed extensively by bears during late July through September (Mattson et al. 1991*b*).

Seeds from whitebark pine are probably the most important food during late summer and autumn for grizzly bears (Mattson et al. 1991*a*). Bears obtain seeds by raiding middens of pine cones cached by red squirrels (*Tamiasciurus hudsonicus*) (Kendall 1983, Mattson and Reinhart 1997). Meat from ungulates also becomes more important during years of poor whitebark pine cone crops (Mattson 1997*a*). Mattson et al. (1991*a*) described other vegetal foods used by grizzly bears. Graminoids and forbs constitute the majority of the summer diet. Bears rely on roots and foliage during autumn when whitebark pine seeds are unavailable.

OBJECTIVES

When we began this project, our objectives were to assess appropriateness (sustainability) of the 6% human-caused mortality value (Harris 1986), using recent data from grizzly bears in the GYE, and suggest revision if necessary. In the course of addressing these questions, we realized that the factors influencing the population's vital rates were diverse and interacted with one another, and any single estimate of sustainable mortality was unrealistic. Thus, we set additional goals of evaluating the population's demographic vigor and understanding important covariates, both intrinsic and extrinsic to the population, well enough to allow for reasonable inference regarding the population's future.

With the advent of more sophisticated models, we explored the influence of an array of temporal, individual, and spatial covariates on demographic vigor. Using these models, we helped explain observed demographic variability and provide insight into the future using short-term projections. During our investigations we confirmed an important relationship between demographic vigor and where a bear resides in the GYE. This potential source–sink dynamic (Pulliam 1988), when coupled with concerns for managing sustainable mortality, has reshaped our thinking about how management agencies might approach management. Consequently, we expanded our initial objective to include an assessment of the current dynamic of the GYE grizzly bear population and to address management considerations for monitoring that may be helpful to the long-term conservation of the species.

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STUDY AREA AND METHODS FOR COLLECTING AND ANALYZING DEMOGRAPHIC DATA ON GRIZZLY BEARS IN THE GREATER YELLOWSTONE ECOSYSTEM

CHARLES C. SCHWARTZ, MARK A. HAROLDSON, AND GARY C. WHITE

Collecting data about birth and death rates is a necessary component of any demographic analysis. We present common elements of field and analytical methods used to estimate demographic parameters and population trends of grizzly bears in the GYE. We describe in detail our study area; methods of capture, handling, and collaring bears; and telemetry studies. We explain our rationale for choosing a specific time series and how we partitioned our sample. We detail how and why we selected covariates used in model building and analytical methods used in model selection. Methods specific to estimation of reproduction and survival are described in the specific chapters.

STUDY AREA

Our study area encompasses the GYE, which includes Yellowstone and Grand Teton National Parks, 6 adjacent national forests, plus state and private lands in portions of Montana, Wyoming, and Idaho. Recent estimates suggest that grizzly bears occupy approximately 34,500 km^2 in the GYE (Fig. 1; Schwartz et al. 2002). A primary component of occupied grizzly bear range within the GYE is the 23,833 km^2 Yellowstone Grizzly Bear Recovery Zone (USFWS 1993).

The GYE is geographically defined as the Yellowstone Plateau and 14 surrounding mountain ranges above 2,130 m (Marston and Anderson 1991) or 1,500 m (Anderson 1991, Patten 1991). We prefer the 1,500 m lower-elevation choice because all 10,022 radiorelocations of grizzly bears in the GYE (1975–2000) were between 1,584 and 3,656 m in elevation (Schwartz et al. 2002).

The GYE contains headwaters of 3 major continental-scale river systems: the Missouri–Mississippi, Snake–Columbia, and Green–Colorado. Aspects of the underlying geology, hydrology, climate, and elevation are described by Marston and Anderson (1991). Long, cold winters and short summers characterize the climate of the Yellowstone Plateau. Precipitation generally increases with elevation and is typically greatest on the windward sides of mountain ranges. Precipitation occurs year round (Baker 1986), with a peak in late spring at low elevations and a peak during summer and autumn for drier areas (Weaver 1980). High elevations have a distinct winter peak in precipitation, particularly in western portions of the GYE (Despain 1987). Average daily maximum and minimum January and July temperatures at Lake Ranger Station near the center of YNP are -5.2, -18.8, 21.8 and 3.5°C, respectively (Temperature and Precipitation Station, Yellowstone Lake, Wyoming, USA, 1948–2001, unpublished data). Precipitation averages 50.8 cm annually, falling mostly as snow between October and April. Frost-free period ranges from 60–90 days at low elevations. In alpine zones, frost may occur throughout the year.

Patterns of precipitation and temperature produce predictable vegetation patterns (Marston and Anderson 1991). Low elevations (<1,900 m) feature foothill grasslands or shrub steppes. With increasing moisture, open stands of juniper (*Juniperus scopulorum*), limber pine (*Pinus flexilis*), and Douglas-fir (*Pseudotsuga menziesii*) occur. Douglas-fir forms the lowest-elevation forest community at around 1,900–2,200 m (Patten 1963, Waddington and Wright 1974, Romme and Turner 1991). Lodgepole pine (*Pinus contorta*) dominates the extensive Yellowstone Plateau at mid-elevations (2,400 m), where poor rhyolite-based soils dominate (Despain 1990). With increasing elevation, spruce–fir or subalpine forests dominate. Engelmann spruce (*Picea engelmannii*) and whitebark pine form the upper tree line around 2,900 m (Patten 1963, Waddington and Wright 1974, Despain 1990). Alpine tundra occurs at the highest reaches of all major mountain ranges.

FIELD TECHNIQUES

Trapping and Collaring

Each year, members of the Interagency Grizzly Bear Study Team (IGBST) radiomarked bears for research and monitoring. Since 1997, grizzly bear capture and handling procedures were reviewed and approved by the Animal Care and Use Committee of the U.S. Geological Survey, Biological Resources Division, Midcontinent Ecological Science Center; procedures conformed to the Animal Welfare Act, and to U.S. Government principles for the utilization and care of vertebrate animals used in testing, research, and training. Captures were conducted under USFWS Endangered Species Permit [Section (i) C and D of the grizzly bear 4(d) rule, 50 CFR17.40 (b)] and YNP Research Permit YELL-00073. We used culvert traps or Aldrich leg-hold snares to capture bears (Blanchard 1985). Trapping was conducted in both front (road access) and backcountry (no road access) settings within and outside national parks and wilderness areas. Trapping occurred principally within YNP during early years, but efforts expanded as bears recolonized habitats outside YNP. All captured grizzly bears, with exception of dependent offspring, were fitted with radiotransmitters. Adults were collared (Telonics, Inc., Mesa, Arizona, USA), whereas independent subadults were instrumented with expandable collars (Blanchard 1985), glue-on, or ear-tag transmitters. Collars were fitted with a biodegradable canvas spacer that ensured collar drop. All transmitters had a motion sensor that reduced pulse rate if stationary for 4–5 hr, allowing for detection of mortalities and shed collars. Additionally, grizzly bears involved in nuisance activity and captured by wildlife management agencies were radio-instrumented.

We flew telemetry flights every 7 to 14 days from mid-April through late November to locate and monitor instrumented bears. We reduced flight frequency from late November through March when most bears denned (Haroldson et al. 2002). Grizzly bears were sighted during approximately 10% of aerial relocations (West 2001, 2002). All transmitters had motion sensors that were designed to change pulse rate if transmitters were stationary. If a pulse rate and location from aerial telemetry indicated a stationary transmitter for at least 2 flights, we visited the site. Stationary signals were usually dropped transmitters, but occasionally we discovered a dead bear or a collar in a condition that indicated an illegal mortality (i.e., cut, shot, buried, or burned).

Data

Time Series. —We began our analysis in 1983 for several reasons:

1. Previous analyses established 1983 as a historic breakpoint for this population (Mattson et al. 1992, Eberhardt 1995, Pease and Mattson 1999).
2. Other publications address demographics during earlier years (Knight and Eberhardt 1984, 1985, 1987) or contrast earlier years (1975–1982) with more recent years (Mattson et al. 1992, Eberhardt et al. 1994, Pease and Mattson 1999, Boyce et al. 2001). Our intent was to evaluate demographic vigor and estimate sustainable mortality based on information collected during a comparable time period.
3. Dump phase-out and closure occurred from 1968 through 1971. During phase-out and following closure, the frequency of problem bears reported in campgrounds increased (Craighead et al. 1995), and there were at least 229 documented grizzly bear deaths (Craighead et al. 1988). By 1979, grizzly bears familiar with sources of unnatural foods within developed areas of YNP appeared to be gone from the population (Meagher and Phillips 1983).
4. Because of continued negative population trend following dump closure, management focused on reducing human-caused mortalities (Knight and Eberhardt 1985). The Interagency Grizzly Bear Committee (IGBC), formed in 1983, recommended that state and federal agencies implement several management actions (Knight et al. 1999, USFWS 2002) to improve grizzly bear survival inside the RZ including YNP. Actions began in 1983 and were incorporated in the 1993 Grizzly Bear Recovery Plan (USFWS 1993). These included policy changes regarding removal versus relocation of problem bears, food storage and garbage disposal restrictions on all federal land within the RZ, elimination or transfer of sheep allotments, and increased law enforcement activities (Interagency Grizzly Bear Committee 1986, Knight et al. 1999).
5. The Yellowstone grizzly bear population declined following dump closure and continued to decline through the early to mid-1980s (Knight and Eberhardt 1984, 1985, 1987). The population began to show signs of recovery in the mid-1980s and continues to increase (Eberhardt et al. 1994, 1999; Eberhardt 1995). The nadir in population size occurred around 1982–1985. Population change from 1975–2002 assumed a more or less open J-shape. Estimating population trajectory over this entire period (decline to the nadir and then upward, i.e., connecting the start and end of the J) is less informative than estimating trajectory from the population nadir around 1983 (bottom of the J). The latter comparison more closely meets our objective.
6. Mattson et al. (1992) compared relative frequency of habituation and food conditioning in Yellowstone grizzlies from 1977–1982 with 1983–1990 and concluded the 2 periods were different ($P = 0.039$), with frequency dropping from 42.7 to 25.9% between the 2 periods.

We used data collected during 1983–2001 in our analyses of survival, but included data from 2002 when analyzing reproduction. We did this because reproductive success in 2002 was determined by environmental covariates from 2001.

Sampling.—Our method of defining our sample differed from previous research using the Yellowstone telemetry data set. The IGBST collared bears for research and monitoring purposes (research bears), whereas management authorities collared bears captured in conflict situations (management bears). Because management bears represented a sample of the population at high risk, inclusion or exclusion in the telemetry sample could influence estimates of survival and population trajectory. Eberhardt et al. (1994), Boyce (1995), Eberhardt (1995), and Boyce et al. (2001) treated individuals trapped for research and those trapped for management purposes as belonging to groups based on circumstances of first capture. Eberhardt (1995) also included some bears caught in management situations in his research sample and "noted that bears caught in 'research' trapping often were caught later for 'management' purposes, and these bears ***are*** included in the survival calculations" (Eberhardt 1995:14). For demographic analysis, both Eberhardt (1995) and Boyce et al. (2001) used survival estimates exclusively from research bears when calculating λ.

In contrast, Pease and Mattson (1999) considered an explicit source–sink demographic model of a population with 2 behavioral types: wary (bears that had never been management-trapped) and conditioned-to-humans (bears that had been management trapped at least once), and used management-trapping rate to estimated the unidirectional rate at which bears moved from the wary to non-wary state. The classification was premised on higher survival for wary bears than human-conditioned bears. Pease and Mattson (1999) deviated from the research–management classification of Eberhardt (1995) and Boyce et al. (2001) and assumed bears caught for research purposes at or near 17 areas of high human density were human-conditioned and thus management-trapped. Cubs born to mothers with prior management actions also inherited their mother's management status, but this assumption was criticized (Eberhardt and Cherry 2000). To accurately estimate survival for the population, the Pease and Mattson (1999) approach to classification of the telemetry sample and their demographic model required estimating flow from wary to non-wary states. Their approach, although novel, required difficult to quantify assumptions about what constituted wary and non-wary individuals, inheritance of non-wary status, and direction of flow from one state to another.

Our analyses used a different approach from that of Eberhardt (1995), Boyce et al. (2001), or Pease and Mattson (1999). Rather than applying a permanent label to an individual based upon where and why it was first captured (research or management), or making assumptions about behavioral traits based upon where an individual was captured (wary or non-wary), we classified bears using a standard sampling approach. We recognized 2 groups of radiomarked bears, which we refer to as our study sample and conflict sample. We avoided the terms research and management to minimize confusion between our sampling approach and those previously reported.

We classified each bear to study sample or conflict sample depending on capture location and telemetry status at time of capture. Under our sampling classification, bears could transfer between samples. Bears first trapped at a study site became part of the study sample. We collared any bear caught regardless of sex, age, or history with the hope that it represented a relatively random sample from the population at large. Bears first trapped at a conflict site by management authorities became part of the conflict sample, a biased subsample of problem bears from the population. However, any member of the conflict sample subsequently caught at a study trap site was reclassified as part of the study sample from that time forward. This allowed bears first caught in conflict situations to become part of our study sample. In contrast, an individual from the study sample subsequently captured at a conflict site retained a study sample classification if wearing a functional transmitter at time of capture (i.e., if part of the study sample at time of conflict-related capture). Only individuals whose collars had failed or been lost (i.e., had been censored from the study sample) and were later captured at a conflict site were reclassified as part of the conflict sample. Our study sample thus contained high-risk individuals, but only those captured from the population at large (i.e., trapped for this study). The proportion of high-risk individuals within the study sample was thus a relatively unbiased reflection of their incidence in the population, neither biased high from the disproportionate number of individuals obtained only from special, conflict-related trapping operations, nor biased low via exclusion of all conflict-trapped animals. That is, the study sample reflected the population at large, whereas the conflict sample reflected a high-risk subgroup. We used information from both samples to build our models, but where sample appeared in any of our best models, we derived model estimates only for the study sample by setting the conflict sample to zero.

We believe our classification avoids problems with previous attempts to divide the telemetry sample into categories based on behavior. Unlike the hard classification of research- or management-trapped, our sample allows bears first captured in a conflict situation to become part of the study sample. This helps avoid under-representing this high-risk subgroup within our study sample when estimating demographic rates for the population. It also avoids the need for assumptions when classifying bears into a wary or non-wary group based upon behavior or location of trapping (Mattson et al. 1992). Such categorization requires knowledge about individuals after trapping and handling and subjective judgment about observed or reported behaviors. This categorization is prone to error if behaviors go unobserved and individuals are inaccurately classified. Our method of classification avoids the need for assumptions about individual behaviors and eliminates any need to estimate flow rates from wary to non-wary state because our study sample should contain a representative mix of behavioral classes.

Issues of Randomness.—Obtaining a random sample from the population of interest is central to making inference. In an ideal world we would obtain a simple random sample from the GYE grizzly bear population. However, this implies that each individual has equal probability of capture (Ratti and Garton 1996), an objective nearly impossible to meet. We know that catchability varies with age, sex, reproductive status, and food availability (Miller et al. 1987, 1997; Schwartz et al. 2003*b*). Additionally, access and terrain influence where and when we can trap, and because bears are not uniformly distributed across the landscape, density likely affects catch success. Such issues of heterogeneity are common to all studies and are generally dealt with by stratifying capture samples by sex, age, or age class, and considering other covariates that influence demographics. The issue of sampling centers on whether our study sample is representative of the GYE population. Telemetry locations from our study sample support the notion that we achieved reasonable geographic coverage. During 1983–2002, IGBST attempted to trap from all occupied areas in the GYE. During 1983–1989, 91.6% of all telemetry relocations fell within the estimated distribution of unique sightings of unduplicated females with cubs (Blanchard et al. 1992) (Fig. 2*a*). Similarly, during 1990–2001, 93.3% of all telemetry relocations fell within the estimated distribution of unique sightings of unduplicated females with cubs (Schwartz et al. 2002) for that decade (Fig. 2*b*). Both figures suggest adequate coverage across the distribution of bears at time of sampling.

As bear numbers and distribution increased, IGBST made efforts to trap in newly occupied habitats beyond the RZ, especially in Wyoming on the southern boundary. Some areas in the GYE were either not trapped or trapping efforts were unsuccessful. These areas included the northern portion of Absaroka Beartooth Wilderness, Pitchstone Plateau, and Centennial and Gravelly Mountains. Efforts to trap and mark bears on Madison and Pitchstone Plateaus during 1992–1994 had little success (1 bear collared). Trapping in the Centennial Mountains of Idaho and Montana during 1991 was unsuccessful. Thus, areas on the perimeter of bear distribution were sampled with limited success, due largely to low bear densities, rather than effort. Bear numbers and density are low on Pitchstone Plateau because of poor-quality habitat associated with rhyolitic flows following volcanic eruptions in YNP. However, there were areas occupied by grizzlies where we did not radiocollar bears, notably the Washakie Wilderness. We speculate that our undersampling from Washakie Wilderness would likely result in a slight underestimation of GYE survival, because individuals living in these remote wilderness areas are probably less vulnerable to humans.

DATA ANALYSES

Covariates

We selected a priori an array of temporal and individual covariates hypothesized to affect reproduction and survival. We began selection using results from other studies of Yellowstone grizzly bears (Craighead et al. 1974; Knight and Eberhardt 1984, 1985; Dennis et al. 1991; Eberhardt et al. 1994; Foley 1994; Boyce 1995; Craighead et al. 1995; Eberhardt 1995; Knight et al. 1995; Pease and Mattson 1999; Boyce et al. 2001) coupled with information on brown and grizzly bears in North America (Craighead and Mitchell 1982, LeFranc et al. 1987, Pasitschniak-Arts 1993, Schwartz et al. 2003 a, *b*). For comparative purposes, we built our models of reproduction and survival with the same suite of covariates.

Temporal Covariates.—We considered year as a covariate in reproduction and survival models for dependent cubs and yearlings, independent subadult, and adults. For survival estimates of independent bears, we incorporated month and season (Table 1), but only considered active and denning seasons for analyses of cub and yearling survival because of data constraints; we set survival to 1.0 for the denning period for cubs and yearlings (Table 1).

Ungulates are an important spring food for post-emergence bears (Green et al. 1997). We hypothesized that survival and reproduction might be higher in years of abundant spring carrion. We used a winter severity index (WSI) (Farnes et al. 1999) as a surrogate for availability of winter-killed ungulates. WSI incorporated minimum daily winter temperature, winter snow pack (in snow water equivalent), and precipitation in the previous June–July (Farnes et al. 1999), and correlates with abundance of ungulate carcasses on winter range in both the Firehole/Norris Basins ($r = 0.80$, $P = 0.0006$) and on the Northern Range ($r = 0.87$, $P = 0.0027$) in YNP (Podruzny and Gunther 2001, 2002). WSI averaged information from 3 elk winter ranges within the GYE lacking winter-feeding programs (Farnes et al. 1999). In theory, WSI can vary from -4 to +4, with 0 indicating an average winter and negative numbers indicating more severe winters. During 1983–2001, the index ranged from -2.2 to 2.2 (Table 2). Female bears were assigned the WSI of their year of breeding (not of parturition) to estimate effects on reproductive output the subsequent year. WSI was assigned to the spring–summer season for adult survival and the active season for survival of dependent young.

Seeds from whitebark pine are one of the most important autumn foods of bears in the GYE, and affect reproduction (Mattson 2000) and survival (Blanchard 1990; Mattson et al. 1992, 2001). Whitebark pine cone production has been estimated annually since 1980 (Blanchard 1990). Nine transects were established in 1983; the number increased to 16 in 1987, and to 21 in 1989. Since 1991, cones have been counted on 18 or 19 transects. We used the median count of whitebark pine cones from transects run annually in the GYE (Haroldson et al. 2003). Because whitebark pine is a masting species (Weaver 2001), with bumper crops of cones produced infrequently in some years and few if any cones produced otherwise, we used median rather than mean counts to avoid skewing the index by extreme counts. Median counts ranged from 0 to 29, with a mean of 7.5 during this study (Table 2). We used whitebark pine index only during autumn for estimates of adult survival and the active season for survival of dependent young.

Previous studies demonstrated a sigmoidal relationship between whitebark pine cone counts and frequency of pine seeds in grizzly bear feces (Blanchard 1990; Mattson and Reinhardt 1994; Mattson et al. 1994, 2001). This function has been described as acute with little use in years when mean counts were <21 cones/tree (Mattson et al. 1994). But autumn use of pine seeds can be heavy when cone crops average >13–23 cones/tree, suggesting uncertainty in the location of the inflection point between low and high use, or that relative intensity with which bears use pine seeds could have changed during their study (Mattson and Reinhardt 1994). Whitebark pine has also been treated as a binomial variable with mast years roughly corresponding to >20 cones/tree (Pease and Mattson 1999). We treated whitebark pine as a continuous variable for 2 reasons: (1) if there is a sigmoidal response in survival as demonstrated for cone counts and consumption rates (frequency in feces), our logistic link function would detect it, and (2) no clear break exists between mast and non-mast years (Mattson and Reinhardt 1994).

Ungulate biomass (UngBio) was derived from annual winter counts of elk from 3 winter ranges (Northern Range YNP, Gros Ventre, and National Elk Refuge) and bison from YNP and Grand Teton National Park. Number of animals by sex and age were determined by multiplying estimated proportions of juveniles, adult females, and adult males by total counts. Total ungulate biomass was computed by multiplying average live weights (for elk, from Houston [1982]; for bison, from P. Gogan, U.S. Geological Survey, personal communication) for each sex–age class by number of individuals, then summing and converting to metric tons. When counts were missing, estimates were interpolated from surrounding years. This covariate was only used in models of survival for independent bears.

We hypothesized that population size of grizzly bears might affect reproduction or survival of dependent offspring in a density-dependent fashion (Miller 1990*a*, *b*, *c*; Boyce et al. 2001). We used counts of unduplicated females (Knight et al. 1995) as an index to population size, using the IGBST rule set to differentiate family groups (Knight et al. 1995). Annual counts of unique females with cubs in the GYE (Knight et al. 1995, Eberhardt and Knight 1996) are summed over 3 years and divided by 0.274, the estimated average proportion of adult females in the population (Eberhardt and Knight 1996), to generate annual estimates of minimum population size. We used these indices of minimum population size as a surrogate of population density and refer to this covariate in models as MinPop.

Counts of unduplicated females were criticized because they can be influenced by effort and sightability (Mattson 1997*b*). To address these issues, Keating et al. (2002) used sighting frequencies to evaluate methods for estimating total number of females with cubs-of-the-year. Such estimates of asymptotic population size are not affected by variation in search effort and sightability (Boyce et al. 2001). Because sighting frequency was most consistent from 1986, Keating et al. (2002) calculated annual estimates of total females from that year forward. We compared unadjusted IGBST counts with Keating's estmates summed over 3 years, divided by 0.274 for years 1986–2001, and found a high correlation between corrected (Keating et al. 2002) and unadjusted counts ($r = 0.86$, $P \leq 0.001$). We also compared slopes of both estimates through time. Because these data were a time series, we tested for serial autocorrelation using the Durbin-Watson (D) statistic. Regressing unadjusted counts against time ($D = 0.90$) indicated first-order autocorrelation ($P < 0.05$). A Cochrane-Orcutt adjustment (Neter et al. 1996) remedied this problem. The D statistic for the corrected data was 0.17, indicating no significant autocorrelation. Slopes of the uncorrected and corrected data were 20.00 (95% CI = 11.02–28.98) and 22.54 (95% CI = 17.83–27.24), respectively. They were not statistically different, and plots suggested quite similar trends (Fig. 3). Consequently, we used unadjusted counts as an index of bear abundance back to 1983 (Table 1).

We used this bear abundance index as a covariate relating bear numbers to reproduction and survival. We believe this index approximated population change because: (1) of nearly identical trajectories of adjusted and unadjusted counts (Fig. 3), (2) independent estimates show the population increased 4–5%/year (Eberhardt 1995, Boyce et al. 2001), and (3) bear distribution expanded during the same period (Schwartz et al. 2002).

Our index of population size reflects bear numbers, not density. Density could be inferred directly from this index if the area occupied during our study remained constant. However, both bear numbers and distribution changed during 1983 to 2002. Schwartz et al. (2002) estimated that the size of the area occupied by grizzly bears during the decades of the 1970s, 1980s, and 1990s was 15,424, 17,086, and 22,904 km^2, respectively. We assumed that area occupied increased linearly during the period and fitted an equation through these 3 data points. Using this fitted equation ($r = 0.95$), we estimated the square kilometers of occupied range annually. We calculated density by dividing minimum population number by range estimate scaled to bears/1,000 km^2. Population density closely tracked the population estimate (Fig. 4).

We used uncorrected counts of unique unduplicated females with cubs from inside YNP and outside YNP to assess population change. We fitted regression lines to the 2 data sets from 1983–2002. We tested for autocorrelation (D statistic, Neter et al. 1996) and compared slopes of the line. Our null hypothesis was that slope = 0, suggesting a stable population, whereas an alternative hypothesis was that slope > 0 indicating an increasing population. Slopes were different if their 95% confidence intervals did not overlap (Fig. 5).

Individual Covariates.—We assigned the individual covariates sample, sex, age, age class, known prior conflicts, and residency to each bear (Table 1). Adult females were assigned an additional covariate to indicate whether they were accompanied by dependent offspring. We use the term 'cub' to refer to bears <1 year old and yearling for bears ≥1 but <2 years old. Our subadult age class included bears 2–4 years old. Bears ≥5 years old were classed as adults, as were 4-year-old females accompanied by cubs. We considered cubs and yearlings as dependent bears, and bears ≥2 years old as independent bears. Residency was formed by 2 variables, each giving the proportion of radiolocations for that bear in 2 geographic zones outside of YNP.

Bears inside YNP have a higher survival rate than bears living outside YNP but within the RZ (Boyce et al. 2001, Johnson et al. 2004). Both of these previous analyses were limited to individuals living inside the RZ (YNP and adjacent lands). We defined a third zone for lands beyond the RZ to fully define our residency covariate. For each bear in each year, we categorized telemetry locations as inside YNP, outside YNP but inside the RZ, or outside the RZ. We treated zones as mutually exclusive and computed proportion of locations in each zone for each bear. Covariate OutYNP was the proportion of annual telemetry locations occurring outside YNP but inside the RZ; OutRZ was the proportion of locations occurring outside the RZ; and InYNP was the proportion of locations within Yellowstone National Park. OutYNP and OutRZ were included together when considered in models, so the proportion of annual locations inside YNP served as the reference.

Cutthroat trout and army cutworm moths are important foods for part of the GYE bear population (Mattson et al. 1991*a*, *b*; French et al. 1994). We considered including these foods as possible covariates in model building. However, unlike whitebark pine, which is probably used by most if not all bears, both trout and moths only occur provincially and are used by only part of the population. Because we lacked a direct measure of use of these resources, we attempted to attribute use through spatial association. For trout, we buffered spawning tributaries of Yellowstone Lake by 2 km during spawning season (May–Jul) and, based on Mattson and Reinhart (1995), assumed any bear in this buffer used fish (1 = use, 0 = no use). Cutworm moths spend the day aggregated under rock and scree in talus slopes, where grizzly bears forage for them (French et al. 1994). For moth foraging, we buffered observations of bears feeding in talus slopes by 500 m and merged these buffers to create moth site polygons. We assumed bears located within these polygons during the season of moth availability (Aug–Oct) foraged on moths (1 = use, 0 = no use).

During 1983–2001, 27 individual bears (86 locations) were located within trout buffers; 9 individuals were represented >1 year. Only 120 bear-months of use of buffers occurred during spawning season, representing 2.0% of total bear-months of availability obtained. Two bears that were located within stream buffers during spawning season died.

During 1983–2001, 30 individual bears (116 locations) were located within moth site polygons; 12 bears were located within polygons during >1 year. Only 141 bear-months of use of buffers occurred during moth season, representing 2.4% of total bear-months of availability. One bear that used moth sites during the season of moth availability died. Based on these statistics, we concluded that we lacked sufficient data to incorporate either cutthroat trout or moths as individual covariates in our models.

Information-Theoretic Methods

We used the information-theoretic approach (Burnham and Anderson 1998, 2002) instead of classical null hypothesis testing. This relatively new paradigm of data analysis is based on the Kullback-Leibler information that avoids many fundamental limitations of null hypothesis testing (Kullback and Leibler 1951). The method focuses on strength of evidence for an a priori set of alternative hypotheses, rather than a statistical test of a null hypothesis. This approach allowed us to rank various models and determine strength of evidence for model selection. We started with a suite of basic models that included covariates clearly identified from the literature as likely affecting reproduction or survival. We then built models of increasing complexity by incorporating additional temporal or individual covariates we suspected might influence reproduction or survival. We did not consider interaction terms because of anticipated difficulty of biological interpretation. We did not attempt to build models with all possible combinations of covariates because this violates the information-theoretic approach.

We selected the best approximating models from the candidate list using AIC adjusted for small sample sizes (i.e., AIC_c) or over-dispersion ($QAIC_c$), where appropriate (Burnham and Anderson 2002). The model with the smallest AIC_c (or $QAIC_c$) was considered the best. We ranked the model with the lowest AIC_c as best and used differences in AIC_c between that model and every other model (ΔAIC_c) to identify other likely models. High Δ_i's were interpreted as less plausible (Anderson et al. 2000). Models having Δ_i within 2 units of the best model were further examined to see whether they differed from the best model by 1 parameter and had essentially the same value of the maximized log-likelihood as the best model. In these cases, the larger model was not supported or considered because inclusion of an additional covariate did not improve model fit to data. We calculated AIC_c weight (w_i) for each candidate model: weights sum to 1 and represent relative likelihood of each model, given the data (Burnham and Anderson 2002). The w_i, called Akaike weights, can be interpreted as approximate probabilities that a model is in fact the Kullback-Leibler best model in the set of models considered. We estimated relative importance of predictor variables x_j by summing Akaike weights across all models in the set where variable j occurred. Thus, relative importance of variable j was reflected in the sum $w_+(j)$ (Burnham and Anderson 2002). The larger the value of $w_+(j)$, the more important variable j was relative to other variables. Using the $w_+(j)$ for all variables allowed us to rank their importance. Burnham and Anderson (2002) caution that when using this sum of Akaike weights [$w_+(j)$], it is important to achieve a balance in the number of models that contain each variable j. We did not do this because to some degree it violates the premise of developing a suite of a priori models.

REPRODUCTIVE PERFORMANCE OF GRIZZLY BEARS IN THE GREATER YELLOWSTONE ECOSYSTEM, 1983–2002

CHARLES C. SCHWARTZ, MARK A. HAROLDSON, AND STEVE CHERRY

Estimates of reproduction and survival are necessary to model grizzly bear demographics (McLellan 1989, Eberhardt et al. 1994, Eberhardt 1995, Hovey and McLellan 1996). Accurate estimates of age at first reproduction, litter size, and interbirth interval are difficult to obtain without a large sample collected over several years to capture environmental variability (Jonkel and Cowan 1971, Rogers 1987, Mattson et al. 1991*a*). An assessment of the long-term reproductive potential of grizzly bears is essential to evaluate factors that might limit population growth and to focus management strategies on those environmental and temporal variables that potentially limit reproductive output.

Recent reviews of literature by Derocher and Taylor (1994), Garshelis (1994), and McLellan (1994) conclude that specific mechanisms of density-dependence in bear populations have not been clearly shown by empirical data for grizzly, black (*Ursus americanus*), or polar (*Ursus maritimus*) bears. However, recent work suggests density-dependent survival might occur in the GYE grizzly bear population (Boyce et al. 2001, Schwartz et al. (2005*a*).

Our objectives were to estimate current values of reproductive parameters for the GYE grizzly bear population. Additionally, we investigated the impact of several covariates on litter production and size to better understand what potentially influenced reproductive performance.

METHODS

Most methods for this work are presented in Schwartz et al. (2005*b*). Specific methods to estimate reproductive rate and model effects of temporal and individual covariates on litter production and size are detailed here.

We visually observed each radiomarked female in our telemetry sample to estimate age at first reproduction, litter size, and litter frequency (Schwartz et al. 2005*b*). Only observations of bears wearing a functional transmitter were included in the sample. In most cases, females were observed multiple times and we obtained complete counts of litter size. A few instances where complete counts were not obtained and the female was not observed again were included in analyses in which reproduction was treated as a binomial variable (cubs or no cubs). If an incomplete count was not noted, but litter size increased with additional flights, we used the larger count to estimate litter size. Reductions in litter size were considered mortalities.

Because bears could have lost cubs before our first visual sighting, our mean litter size and fecundity rates are potentially biased low. To determine the magnitude of bias, we estimated mean date of first observation of all females with cubs and compared this to the date we first observed a female with cubs. Our first observation of a female with cubs approximated the known den emergence date (Haroldson et al. 2002). Using mean date of first observation, we back calculated expected number of cubs that should have emerged from the den by dividing number seen by the survival rate calculated over this period (emergence day minus mean emergence day). This assumes survival rates pre- and post-emergence are equal, something we lack empirical data to test. This effectively adjusted our counts of cubs lost between emergence and first sighting. Our estimate of daily survival and mean date of observation were derived from information used to calculate cub survival rates (Schwartz et al. 2005*a*).

We used the method of Garshelis et al. (1998) to calculate mean age at first reproduction. This method generates an unbiased estimate of the mean age of primiparity using data from bears that do or do not produce cubs. We used bootstrapping (Efron and Gong 1983) to estimate standard errors and the 95% confidence interval. We calculated bootstrap estimates in Microsoft Excel (Microsoft, Redmond, Washington, USA) using program PopTools add-in (G. M. Hood, 2004. PopTools version 2.6.2. http://www.cse.csiro.au/poptools). We iterated (*n* = 500) the estimate of the mean and SE, which stabilized at *n* = 300. We only included in our analysis those females that were monitored continuously from age ≤4 years old (earliest age of first litter production) until they produced their first litter or were censored (lost or dead collar) from the sample.

We calculated reproductive rate (female cubs/female/year) using methods outlined by McLellan (1989) and Eberhardt (1995). Eberhardt (1995) estimated population-wide reproductive rate by calculating a mean of the observed reproductive rates for each adult female (≥4 years old), regardless of the number of years she was observed or litters she produced. Cub production rate for each female is calculated as total cubs produced divided by the number of years she was sampled. A mean of these rates gives equal weight to each female, thus the sample unit in this case is an individual female. McLellan's (1989) method treats each female in the sample as a record (mean rate/female as above), but weights each record based upon the number of years a female was observed. The estimate derived by this method is identical to the bear-year sample unit of McLellan (1989) except that the standard error and confidence interval is based on *n* individuals rather than *n* bear-years. Like Eberhardt et al. (1994), we assumed a 50:50 sex ratio at birth and, therefore, divided the estimate by 2 to obtain female cubs/female/year. The sex of 1,326 cubs born in zoos was 51% male (USFWS 1993: Appendix C).

We calculated interbirth interval using the Garshelis et al. (1998) method to estimate age at first reproduction. This produced similar unbiased estimates because it treated each interval (complete or incomplete) as a sample. We used jackknife techniques to estimate variance.

We investigated the probability that females would produce a litter of cubs if they were available to breed. We considered breeding-aged females (≥3 years old) available to breed if they were alone or accompanied by 2-year-olds. Females assumed unavailable to breed were those accompanied by cubs or yearlings. For females available to breed in year *t*, we classified the outcome of each breeding event the following year (*t* + 1) as a binomial (1 = cubs, 0 = no cubs). If the outcome was cubs, we included a count of litter size. Because females can produce their first litter any time between 4–7 years of age, we created age classes of 4, 5, 6, and ≥7. Because earliest age of first litter production is 4, we used the estimate generated for age at first litter production using the method of Garshelis et al. (1998) for this age class. However, because the probability of producing a litter after age 4 is not identical to the proportion of females producing their first litter after age 4 (after age 4, some females can lose a litter and breed again), we calculated probability of successful breeding as the number of successes divided by total number of bears available to breed. We calculated a 95% confidence interval with 1,000 bootstraps of the raw data. We treated each observation of a female from the year of breeding through the following year with cubs or alone as an independent observation.

We assigned covariates to each breeding event in an effort to assess what factors influence reproductive success. Temporal covariates assigned to the year of breeding included indices of population size, whitebark pine cone production, and winter severity. Individual covariates included sample, litter size, mother's age and age squared, and our residency covariate. Detailed descriptions of each covariate are in Schwartz et al. (2005*b*).

We evaluated the probability (*P*) of producing a 0-, 1-, 2-, or 3-cub litter relative to these covariates using multinomial logistic regression. Multinomial logistic regression is a generalization of binary logistic regression to settings involving a response variable *Y* with *J* > 2 categories. For our data, *J* = 4 and the response is coded as 0, 1, 2, or 3 depending on observed litter size. We chose to model response using a baseline-category logit model (Agresti 1996:206). Given a vector of explanatory covariates $\mathbf{x} = \left(x_1, x_2, \cdots, x_p\right)$, the response is modeled as:

$$P\left(Y = j \mid \mathbf{x}\right) = \frac{\exp\left(\alpha_j + \beta_{j1}x_1 + \cdots + \beta_{jp}x_p\right)}{\sum_{k=1}^{J} \exp\left(\alpha_k + \beta_{h1}x_1 + \cdots + \beta_{hp}x_p\right)}$$

for $j = 1, 2, \cdots, J$. A baseline category is chosen and the parameters for that category are equal to 0. If category *J* is the baseline then $\alpha_J = \beta_{J1} = \beta_{J2} = \cdots = \beta_{Jp} = 0$. The model reduces to ordinary binary logistic regression when *J* = 2. The baseline-category logits are

$$\log\left(\frac{P\left(Y = j \mid \mathbf{x}\right)}{P\left(Y = J \mid \mathbf{x}\right)}\right) = \alpha_j + \beta_{j1}x_1 + \cdots + \beta_{jp}x_p$$

for $j = 1, 2, \cdots, J$. The parameters are estimated simultaneously via maximum likelihood method. We modeled *Y* as a nominal response variable, although strictly speaking, it is ordinal. The most common method is the proportional odds model (Agresti 1996). A key assumption of this model is that a single slope parameter for all categories exists; we did not believe this assumption was valid for our data. We use the ordinal nature of the response variable informally in interpreting results (Agresti 1996). We tested model fit as per Hosmer and Lemeshow (2000).

RESULTS

Age of First Reproduction

During 1983–2002, we observed 40 females (≤4 years old) until they either produced a litter (*n* = 22) or were censored from the sample before producing their first litter (*n* = 18). Mean age of first litter production was 5.8 years (Table 3). The proportion of females within an age that produced their first litter of cubs at that age (4, 5, 6, and ≥7) were 0.10, 0.30, 0.56, and 1.00, respectively.

Litter Size

We observed 108 individual adult female bears (>3 years old) for 329 bear-years and documented the production of 104 litters. We obtained counts of cubs for 102 litters for 327 bear-years. The mean length of monitoring/female was 3 years (SE = 0.19, *n* = 108, range 1–13).

We detected no difference in litter size of cubs-of-the-year (95% CI for difference = -0.14–0.42) between the study sample ($\bar{x}$ = 2.14, SE = 0.11, *n* = 29) and conflict sample ($\bar{x}$ = 2.00, SE = 0.08, *n* = 73); the mean of the pooled data was 2.04 cubs/litter (SE = 0.06, 95% CI = 1.92–2.16, *n* = 102). The proportions of litters with 1, 2, and 3 cubs were 0.18, 0.61, and 0.22, respectively. We did not observe any 4-cub litters, but we know they occurred because we captured a female with 4 yearlings.

We detected no difference in litter size of yearling offspring (95% CI for difference = -0.43–0.69) between the study ($\bar{x}$ = 2.03, SE 0.13, *n* = 37) and conflict ($\bar{x}$ = 1.90, SE = 0.16, *n* = 20) samples; the mean of pooled data was 1.98 yearlings/litter (SE = 0.10, 95% CI = 1.79–2.18, *n* = 57). Proportion of litters containing 1, 2, 3, and 4 yearlings was 0.26, 0.51, 0.21, and 0.02, respectively.

Breeding Probability

We did not detect a difference (95% CI for difference = -0.13–0.10) in the proportion of females accompanied by cubs in our study ($\bar{x}$ = 0.31, *n* = 240) and conflict ($\bar{x}$ = 0.33, *n* = 89) samples, so we pooled our data. We only present information from this pooled data set. The proportion of all females age 4 or older (*n* = 104) accompanied by cubs in the sample of radiomarked females (*n* = 329, annual range 6–30) varied among years (Fig. 6) from a low of 0.05 to a high of 0.60; the mean (104 cub litters/329 bear-years) was 0.316 (± 0.026).

Reproductive Rate

Reproductive rate (female cubs/female/year) varied little with method of calculation. Weighting on females and on female-years provided estimates of 0.309 and 0.318, respectively (Table 4).

We estimated error due to cubs that might have died before we observed them. The mean day of first sighting was 65 days post emergence, assuming 22 April as the day of emergence, which was set as day 1 in our survival program. Applying a mean daily survival rate of 0.998093 (Schwartz et al. 2005*a*), survival from day 1 to day 65 would be 0.8833. This implies that the 208 cubs observed were the survivors out of an estimated 235 (208/0.8833) cubs alive at den emergence. In turn, 235 cubs produced during 327 bear-years equates to 0.362 female cubs/female/year (235/327/2), which suggests that our estimated reproductive rate may be biased about 13% low due to loss of cubs before observation.

Interbirth Interval

Our estimate of interbirth interval was 2.78 years (approximate 95% CI = 2.48–3.08) (Table 4). Alternatively, we calculated the interval as the reciprocal of litters/year, thus providing an estimate of years/litter. We observed 104 cub litters/329 bear-years (0.316 ± 0.03 SD), providing an estimate of 3.16 years/litter. Giving each female equal weight (0.305 litters/female/year) provides an estimate of 3.28 years between litters. Estimates of years/litter are not equivalent to interbirth interval because calculations contain some nulliparous females or females producing a litter but not completing an interval. Our estimates of years/litter thus approximate litter frequency from our telemetry sample for bears ≥4 years old.

Probability of Litter Production

The probability (95% CI) of a female breeding given that she was available to breed was 0.350 (0.15–0.55), 0.526 (0.316–0.789), 0.529 (0.294–0.765), and 0.636 (0.527–0.764) for age classes 4, 5, 6, and ≥7, respectively. The estimated proportion of females breeding at age 3 was 0.098 (0.025–0.200) (Table 3).

The best model explaining the probability of a female producing a litter of a given size (Tables 5 and 6) included a single covariate (minimum population size) to describe variation in litter size (Fig. 7). Our results indicated that for each 10-bear increase in our index of population size, the odds of a 1-cub litter being produced were 1.21 (95% CI = 1.06–1.39) times the odds of a 3-cub litter being produced. The estimated odds for 0- or 2-cub litters versus a 3-cub litter were 1.13 (1.01–1.26) and 1.14 (1.02–1.28) times, respectively, for each 10-unit increase in our population index. The 0-cub litter curve was slightly curvilinear. For our best model, the 95% confidence intervals for the coefficients and odds ratios did not bound 1, leading us to conclude we detected statistically and biologically significant relationships.

The second-best model added median whitebark pine cone counts as a covariate (Tables 5 and 6). Other models had considerably weaker support than our top 2 models. Female age appeared in the third-best model and winter severity in the fourth (Table 5). Covariates not supported as being important were residency, age squared, and sample. Based on ΔAIC_c and AIC_c weights, our top 2 models were nearly identical. Results indicated that for each unit increase in median counts of whitebark pine cones, the estimated odds of a 1-cub litter being produced was 0.89 (95% CI = 0.78–1.02) times the odds of a 3-cub litter being produced (Table 6). The estimated odds of either a 0- or 2-cub litter being produced were 0.97 (0.91–1.04) and 1.01 (0.95–1.04) times, respectively, the odds of a 3-cub litter being produced. The 95% confidence interval for whitebark pine β coefficients and the subsequent odds ratios bounded 1; however, when plotted, the most striking effect of changing cone counts relative to our population index was associated with 1-cub litters (Fig. 8*a*). Our goodness-of-fit-statistics (Table 6) indicated that our models reasonably fit the data. In addition, our summary measures including Somers *D*, the Goodman-Kruskal gamma, and Kendall's tau-a indicated the models were a good fit to the data.

Increasing population size reduced the probability that a female would produce a 3-cub litter and increased the probability that she would produce a 1-cub litter (Fig. 7). Our second-best model suggested that the influence of increasing population size was manifested to a greater degree in the production of a 1-cub litter when median whitebark pine cone production was low as opposed to when the median whitebark pine count was high (Fig. 8*a*). There was a lesser effect on the production of 3-cub litters with low versus high cone production. We combined probability curves for females producing a 0-, 1-, 2-, or 3-cub litter into a single line to predict mean litter size (Fig. 8*b*) as a function of population size and whitebark pine cone abundance. Effect of population size appears asymptotic as population size increases, with smaller mean litter sizes occurring following years of poor cone production.

DISCUSSION

Our estimate of mean age at first production (5.8 years) was slightly older than the estimate (5.7 years) provided by Craighead et al. (1995:412) and the estimate provided by Eberhardt (1995) of 5.6 years from the GYE. Eberhardt's (1995) estimate was based on completed intervals, whereas Craighead et al. (1995) included incomplete intervals inferred to be completed the following year. Such estimates of age at first reproduction tend to be biased low (Garshelis et al. 1998). Our estimate falls within the range (4.4–8.1 years) in the literature (McLellan 1994, Schwartz et al. 2003*a*). Our sample suggested that nulliparous females produce a litter by age 7. However, with a sample size of 40 and only 3 nulliparous females producing their first litter at age 7, we may have missed females that produced their first litter at an ages >7.

Mean litter size of 2.04 was comparable to the mean of 2.10 presented by Craighead et al. (1995:417) for the GYE from 1975–1989. Litter size for grizzly bears from our study area fell within the reported range of 1.7–2.5 (McLellan 1994, Schwartz et al. 2003*a*). Craighead et al. (1995) categorized bears into age classes of 4–8, 9–14, 15–20, and 21–25 and calculated mean litter size for each age class as 2.00, 2.44, 2.00, and 1.33, respectively. For comparison, we calculated means for these same categories. Ours were 1.96 (SE = 0.085, *n* = 53), 2.12 (SE = 0.113, *n* = 33), 2.07 (SE = 0.153, *n* = 15), and 3.0 (SE = 0, *n* = 1), respectively. Mean litter size for the 9–14 year age class for both data sets tended to be larger than mean litter size for the other age categories, suggesting that these females are at their reproductive prime. However, for both data sets, the calculated 95% confidence intervals for all age categories overlapped, indicating no statistical difference among age categories or periods. Detecting slight shifts in mean litter size among ages or age classes, especially when other environmental variables affect litter size, requires a very large sample because of narrow variation in litter size. Female age appeared in our third-best model, providing support for increased litter size with age. This effect was manifested as an increase in 3-cub versus 2-cub litters as female age increased. The biological trend of greater production in prime-aged females also was supported by analyses of reproductive performance in brown bears presented by Schwartz et al. (2003*b*) for a metadata set containing 4,726 observations. They detected differences in litter production among different-aged females, with peak litter production occurring from 8 to 25 years of age. Schwartz et al. (2003*b*) only considered the probability of a female producing a litter and did not address litter size. Their results also suggested senescence in litter production occurring around age 25. The covariate age squared did not appear in our top models. We anticipated this because we had virtually no old (>20 years old) females in the sample, with none beyond 22 years old.

The probability that a female available to breed was observed with cubs the following year varied considerably. Some of this variation was due to small sample sizes in some years, but biologically one would expect litter production to vary with food availability (Nagy et al. 1983, Case and Buckland 1998). Indeed, our second model strongly suggested that litter size declined as median whitebark pine cone production declined. Typically, a year with a low proportion of females accompanied by cubs (e.g., 1985 and 1995) was followed by a year of high production. However, it appears that litter production (as opposed to litter size) was influenced by factors other than abundance of whitebark pine, as suggested by the relatively weak correlation between median cone production the year of breeding and litter production the following year ($r = 0.393$, $P < 0.05$, $n = 19$). We suspect that females available to breed do so under most circumstances but that litter size is influenced by availability of high-quality foods (i.e., seeds from whitebark pine cones). Failure of most females to produce a litter in some years is probably triggered by a catastrophic crash in the availability of most if not all important autumn foods during the year of breeding. On average, a female produced a litter every 3.16 years.

Our estimate of reproductive rate using female-year (0.636) and individual females (0.619) as the sampling units did not differ from the estimate of Craighead et al. (1995:420) for the GYE ($\bar{x} = 0.61$, SE = 0.07), or the estimate (0.328 female cubs with 50:50 sex ratio = 0.656 cubs of both sexes) used by Eberhardt et al. (1994) to model the GYE population. Our estimates of reproductive rate fell within range of estimates reported for other brown and grizzly bear populations (0.42–0.87) (Case and Buckland 1998, Schwartz et al. 2003*a*).

Our multinomial logistic regression analysis suggested that litter size is sensitive to population size (i.e., density). To our knowledge, this is the first quantitative link between population size and reproductive performance in a grizzly bear population (Taylor 1994). Our results suggest that as population size increases in the GYE, the probability of a female producing a 3-cub litter declines and the probability of her producing a 1-cub litter increases.

These results suggest we might be seeing a density-dependent response in reproduction. However, because of the way we collected our data, we also might be observing a density-dependent response in survival. We did not observe the number of cubs produced by each female in the den, and therefore cannot discount early mortality. Additionally, because we did not observe all females immediately upon den emergence, we might have missed some post-emergent mortality. Consequently, we might be measuring perinatal mortality as opposed to a density-dependent response in the number of cubs born. Regardless, our models suggest a need to include density-dependence when modeling the GYE grizzly bear population.

We do not believe that our findings suggesting density dependence are spurious or related to another time-correlated covariate we did not include or measure. As discussed in Schwartz et al. (2005*b*), we chose our covariates following considerable discussion. We chose not to include measures of some important foods because we lacked empirical data to do so. However, we would not expect cutthroat trout or cutworm moths to either increase or decrease linearly from 1983 through 2002. We know cutthroat trout numbers have declined recently, but only after increasing in abundance following changes in fishing regulations (Gresswell and Varley 1988). We also know that cutworm moth abundance, as measured by use at known moth sites, fluctuated during our study (Bjornlie and Haroldson 2003). There was also a possibility that age structure of the population changed during our study. Because the population was growing, one might hypothesize that mean age structure declined. Declining age in the adult female segment of the population could result in smaller mean litter size because young females tend to produce smaller litters than older females. However, age structure of our sample varied widely from 1983 to 2002 (mean age in years = 7.8, SD = 4.0, range 4–12) with no consistent trend either downward or upward, eliminating concern that changing age structure was a spurious correlate.

Our multinomial models support density dependence in reproductive output in female grizzly bears. Eberhardt (1977) hypothesized that compensatory responses in large mammals operate in a sequence, with survival of adult females the last to change as a population increases. He postulated that population regulation was largely a consequence of changes in survival of young animals followed by changes in reproductive rates. Life-history strategy of bears emphasizes a long life to reduce impacts of variability in recruitment rates and cub survival (Taylor et al. 1987, Taylor 1994). Taylor et al. (1987) emphasized that cub production and cub and yearling survival were the most likely parameters to be reduced by density effects. They further stressed that parameters most likely affected by density were those likely influenced by environmental variation. Our results and those of cub and yearling survival (Schwartz et al. 2005*a*) support these hypotheses.

Based on $\Delta \mathrm{AIC}_{c,}$ and AIC weights, our top 2 models were nearly identical. Our indices of population size and whitebark pine cone production in the year of breeding influenced litter production (Fig. 8). Increasing availability of whitebark pine seeds in the year of breeding has a positive effect on the likelihood that a female would produce a 3-cub litter (Mattson 2000); pine seed consumption for individual bears was based on observed or inferred feeding habits from scat and field sign at telemetry locations. We set our whitebark pine index the same for all females in a given year, thus assuming that pine nut consumption for all females in a given year was identical or nearly so. Our index of pine nut use was coarser than Mattson (2000) and might explain reduced significance of this covariate in our model. Recent advances in stable isotope analysis (Felicetti et al. 2003) allow us to measure pine nut consumption among individuals from hair samples, thus avoiding estimating diets by visiting feeding sites and collecting feces. Application of these methods to future demographic models should improve our understanding of the contribution of important foods to reproductive performance of individual females.

The temporal and individual covariates we used improved our understanding of influences on grizzly bear reproduction. Both Schwartz et al. (2005*a*) and Haroldson et al. (2005*a*) detected a relationship between cub, yearling, and adult GYE grizzly bear's residency and their survival rates. We did not detect a similar response with this spatial covariate and reproduction. The models containing this covariate (OutYNP and OutRZ; Table 5) had a $\Delta AIC_c \geq 6$, suggesting considerably less support for these models.

MANAGEMENT IMPLICATIONS

To our knowledge, this is the first quantitative analysis that suggests a relationship between grizzly bear density and reproductive output. These results are intriguing and support the concept of compensatory mechanisms in grizzly bear reproduction. These mechanisms suggest flexibility in life-history parameters that maintain a balance between population density and resource availability. Bear biologists have long suspected the existence of such regulatory effects in bear populations, but have failed to detect them (Taylor 1994), although bear numbers, like other large mammal populations, must ultimately be regulated by density-dependent factors (Taylor 1994). Our results suggest that compensatory mechanisms in the GYE grizzly bear population should be considered in management programs. In estimating sustainable human-caused mortality, for example, it would be inappropriate to project over long periods if the population is increasing or decreasing. Sustainable mortality should be updated as new demographic information becomes available.

Our results provide insight on potential impacts of relative changes in food availability on grizzly bear demographics in the GYE. For example, white pine blister rust (*Cronartium ribicola*) has the potential to eliminate whitebark pine seed production in the long-term (Kendall and Keane 2001) and thus reduce overall reproductive performance in the GYE grizzly bear population. Although our data represent a time series and were not collected in an experimental manner (no whitebark pine seeds compared to whitebark pine seeds), they do provide insight into potential consequences of the loss of pine nuts to bears. Bear management plans should be designed to respond to these changes.

SURVIVAL OF CUB AND YEARLING GRIZZLY BEARS IN THE GREATER YELLOWSTONE ECOSYSTEM, 1983–2001

CHARLES C. SCHWARTZ, MARK A. HAROLDSON, AND GARY C. WHITE

Estimating juvenile survival rates is a necessary component of evaluating the demographic vigor of a population (Caughley 1977). Many methods are used to estimate survival of large mammals, and most employ a sample of radiomarked individuals (White and Garrott 1990). Application of such techniques requires regular monitoring of marked individuals to determine their fates. With dependent offspring, particularly in large carnivores, marking is not always practical. Consequently, marked adult females are observed with dependent young to estimate survival. Such an approach has been used successfully to estimate cub and yearling survival in both black (Schwartz and Franzmann 1991, Doan-Crider and Hellgren 1996) and grizzly bears (McLellan et al. 1999, Schwartz et al. 2003*a*:Table 26.6) where sightability is reasonably good.

Our objectives were to provide current estimates of survival rates for cubs and yearlings that could be combined with recent estimates of adult survival (Haroldson et al. 2005*a*) and reproduction (Schwartz et al. 2005*c*) to approximate sustainable human mortality for the GYE grizzly bear population. Additionally, we investigated several individual and temporal covariates to better understand their influences on survival of dependent young in the GYE.

METHODS

Most methods are presented in Schwartz et al. (2005*b*). Here, we detail specific methods used to estimate survival of dependent young and model the effects of temporal and individual covariates on survival.

Survival

We used the software package Program MARK (White and Burnham 1999) with nest success data type (Dinsmore et al. 2002) to estimate daily survival rate of dependent offspring (cubs and yearlings). The nest success data type allows for irregular observations and only requires information on when the individual was first observed, last observed alive or censored, and its final fate (alive or dead). Thus, the nest success data type accommodates intermittent observations available for dependent offspring and a lack of knowledge of exact date of death. The program also allows inclusion of individual covariates and separation of observations into various attribute groups (i.e., year of observation, sex, and capture status).

Our input data consisted of records grouped by categories, with each record consisting of 5 values (Dinsmore et al. 2002): (1) first day a female bear and a dependent young were observed, labeled time *i*; (2) last day a dependent offspring was known to be present with its adult female, labeled time *j*, which for young that survived to become yearlings would be the start of hibernation as yearlings; (3) last day that an adult female was monitored, labeled time *k*. Time *k* for cubs or yearlings that survived was the same as time *j*, i.e., the day that the young entered hibernation. For cubs or yearlings that died, time *k* was the first observation of a female without dependent young; (4) fate of the young: $f = 0$ (survival), and $f = 1$ (mortality); and (5) number (frequency) of young that had that history. Individual covariates were allowed after the 5 required variables.

The likelihood constructed from these values was

$$L = \prod_{i=l}^{j-1} S_l \left(1 - \prod_{l=j}^{k-1} S_l \right)^f ,$$

where the first product was the likelihood of surviving from time *i* to *j*, and 1 minus the second product was the likelihood of dying during the interval *j* to *k*. Note that for fate $f = 0$ (i.e., young survives), $j = k$, so that the second term did not enter the likelihood for young that survived. Because exact date of mortality was unknown, the survival analysis performed here was not feasible with logistic regression and requires the approach of Dinsmore et al. (2002). The resulting estimate of survival was unbiased, assuming survival was constant over the interval from time of den emergence until entry into the sample. It was also unbiaded because we estimate mortality conditional on being alive, entered into the sample, and with a known interval in which death occurred. The model in Program MARK, an extension of the Mayfield estimator (Mayfield 1961, 1975), handled the inexact time of death and was based on probability of daily survival. When an animal died in a multi-day interval, probability of mortality was taken as 1 – (probability of surviving the interval).

We did not conduct goodness-of-fit (GOF) tests for survival estimates because they are problematic. GOF is computed based on the difference between a hypothetical, parameter-saturated model and the most complex (global) model considered in the set of models analyzed. The parameter-saturated model is the one where each data point is fit perfectly (i.e., the number of parameters in the model equals the number of data points). The saturated model is of no interest in the analysis because it is over-parameterized. However, for models presented here, the saturated model is of interest. The basic model used in all of our survival analyses is the binomial distribution. For *n* animals, the estimated survival during an interval is the number living through interval (*y*) divided by number alive at the start of the interval, $\hat{S} = y / n$. This simple model is the saturated model, since no model with more parameters can explain the observed value *y* (assuming that no additional information is available on *n* individuals). As a result, the global model considered in our analyses is also the saturated model and fits the data perfectly. No GOF test is possible. We did use number of cubs within litters to compute a GOF statistic and then used this result to compute a factor $(\hat{c})$ to correct for over-dispersion in the analysis.

We treated individuals within a litter as independent observations (i.e., different nests). When litter size declined, or a female was observed without dependent young, we assumed them dead. This assumption was likely true for cubs-of-the-year, but may not have been correct for females with yearlings. We know that some females wean offspring as yearlings (Blanchard and Knight 1991, Craighead et al. 1995:Table 17.8), but we do not know the fate of these weaned individuals. We lack data to make any objective decision on the proportion that might survive. Hence, we assumed all yearlings that disappeared from their mother died. This likely makes our estimates of yearling survival lower than had we known the fate of every individual.

We divided our observation period into 3 intervals. Our first observation of a female with cubs occurred on 22 April (Julian day 112) and the last female observed with cubs-of-the-year before den entrance occurred on 1 December (Julian day 335). The first observation of a female with yearlings occurred on 5 April (Julian day 95) and the last day of observation occurred on 22 October (Julian day 295). We set the start day for the nest survival program at day 1 (Julian day 112) and ended the interval on day 224 (Julian day 335). The second interval (denning) began on day 225 and ended on day 348 (Julian day 94). The third interval started on day 349 and continued through day 549. Program MARK estimates daily survival. We determined survival for each period by raising the daily survival estimate *i* to the power for the number of days in that interval. Our survival intervals were 224, 124, and 200 days for cub, denning, and yearling survival, respectively.

Because each record in the program was an individual cub or yearling and each was assumed to be a random sample, we used a Chi^2 GOF test to evaluate if the distribution of mortalities was random among litter sizes and estimate the over-dispersion parameter $(\hat{c})$. We computed separate GOF statistics for cubs and yearlings because we anticipated different survival rates for these groups. For each litter size, we computed the expected number of litters that would exhibit the range of mortalities (e.g., for a 3-cub litter, possible mortalities are 0, 1, 2, or 3) based on the overall cub or yearling survival rate. Overall survival rate was the number of cubs or yearlings that lived divided by the sample total. For example, we computed expected number of 3-cub litters with 1 mortality by taking the number of 3-cub litters times survival rate squared (for the 2 surviving cubs) times 1 minus survival rate (for the deceased cub) times 3 (because there are 3 possible ways that 1 cub out of 3 could die). The Chi^2 statistic was computed as the sum over all cells of $(\text{observed - expected})^2/\text{expected}$. Because we had small sample sizes in some cells, we pooled litters of 3 with 2 and 3 deaths into single categories for cubs and yearlings. We also pooled 2-yearling litters with 1 and 2 deaths. We calculated 2 Chi^2 statistics for cubs and 2 for yearlings because we had 5 bears that, based on our observation sequence, could have died either as cubs or as yearlings. We treated these 5 individuals as if they died as cubs or died as yearlings. We observed 137 cubs from 65 groups and documented 32 mortalities. We also observed 73 yearlings from 36 groups and documented 5 mortalities. Total mortalities in the data set equaled 42 (32 + 5 + 5). For one analysis, we treated cub deaths equal to 37 and yearling deaths equal to 5. In the alternate analysis, we treated cub deaths equal to 32 and yearling deaths equal to 10. We combined our Chi^2 statistics for cubs and yearlings for each of the 2 alternative data sets into a common statistic by summing both the Chi^2 and the degrees of freedom. Dividing the sum of the Chi^2statistics by the sum of their degrees of freedom provided us with an estimate of over-dispersion or extra binomial variation. We used the mean of this statistic from the 2 alternative data sets to adjust the quasi-likelihood estimate $(\hat{c})$ in Program MARK. We also examined effect of litter size on survival as an individual covariate within our models.

Factors Affecting Survival

We used the logit link function in Program MARK for our analyses. When the mean value of individual covariates is very large or small, or range of the covariate is over several orders of magnitude, the numerical optimization algorithm in Program MARK may fail to correctly estimate parameters. To avoid this, we standardized values of individual covariates by the transformation:

$$(x_i - \bar{x})/\mathrm{SD}$$

i.e., transformed means were zero, and individual values varied from approximately -3 to +3. Individual covariates that were scaled in our models were residency statistics (OutYNP and OutRZ), litter size, and female age. Temporal covariates were not standardized.

As per Burnham and Anderson (2002), we developed a list of a priori covariates based on information about the GYE grizzly bear (Schwartz et al. 2005*b*). Individual covariates included residency, litter size, mother's age and age squared, and classification into study or conflict sample. Temporal covariates included our indices of whitebark pine cone production, winter severity, and population size. We included our index of whitebark pine cone production, during the year of breeding and pregnancy, hypothesizing that autumn food could impact a female's fat reserves and ultimately her ability to lactate and rear cubs the following year. Such a model would detect the influence of cone production on cub survival as determined by the female's condition the previous year. Likewise, a good crop of whitebark pine seeds during the year a cub is born can influence its survival as a yearling. We also looked at effects of cone production on survival in the same year. We hypothesized that cubs or yearlings might fare better in years of abundant winter carrion, although some evidence indicates they might fare worse (Mattson 2000). Grizzly bear population size might affect cub survival in a density-dependent fashion (Miller 1990*a*, *b, c*; Boyce et al. 2001).

Sexually selective infanticide theory (Hausfater and Hrdy 1984, Swenson et al. 1997) suggests that cub mortality can increase following removal of male bears, especially adult males. An opposing hypothesis is that greater mortality of adult bears can result in increased survival of young bears, particularly cubs (Miller 1990*b*). We tested the influence of male removal on survival of cubs the following year using individuals in our study sample. We tested both total (all age classes) and adult male mortalities as recorded for the GYE (Craighead et al. 1988, Haroldson 2002). We only included cubs classified in the study sample because most cubs in the conflict sample died of human causes.

RESULTS

Between 1983 and 2002, we collared and monitored 108 individual female bears observed for 329 bear-years. During this time they produced 104 litters of cubs. We obtained useful data from 49 unique radiocollared adult females with cubs and yearlings. Most females (74%, *n* = 36) were observed with only 1 litter, but 20% (*n* = 10) and 6% (*n* = 3) were observed with 2 or 3 litters, respectively. Our sample contained 137 dependent young from 65 litters. We documented 42 mortalities (Table 7), with the majority being cubs that died during autumn, when bears are hyperphagic (Mattson et al. 2003). Cause of death was known for 10 of 32 cub mortalities; all were human-caused and associated with management actions directed at the adult female due to conflict with humans. Six deaths were directly attributable to management removal (euthanasia or removal to a zoo, which is equivalent to death in this study), 1 was an accidental death during a management capture operation, and 3 were cubs that disappeared shortly after transportation with their mother from a conflict site: all were presumed dead. For only 1 of 5 cases where yearlings were presumed dead was the cause of death documented; a yearling was removed due to management problems and sent to a zoo. In all other cases, the cubs or yearlings disappeared and were not observed when visual sightings were made of their mother; all were presumed dead.

Survival of individual cubs and yearlings from litters of different sizes was not random ($Chi^2 = 31.5$, $P \leq 0.003$). We also recognized that survival of cubs within a litter was not statistically independent. Violation of the assumption of independence results in unbiased estimates of survival, but variance of estimates is too small. To understand this, consider that the litter is the true sampling unit, rather than cubs. The effect is to reduce sample size considerably, so sampling variance is larger for the estimate based on litters as opposed to the estimate based on individuals where sample size is larger. The approach we used compensates for this violation. Our computed variance inflation factor, $\hat{c}$, inflates variance estimates obtained using cubs as the sampling unit. We used 2.434944 for $\hat{c}$ to adjust for over-dispersion in the quasi-likelihood; this value is reasonable as it is close to the mean litter size.

The best-fitting model (Table 8) had 4 parameters and detected variation in survival between ages of dependent young (cubs vs. yearlings) and adult female residency (Fig. 9). Mean estimated yearling survival (0.817, CI = 0.489–0.944) was higher than for cubs-of-the-year (0.640, CI = 0.443–0.783), although the 95% confidence intervals overlapped. Our best models indicated cub and yearling survival were most affected by residency. Survival was highest for cubs and yearlings (0.827 and 0.917, respectively) living outside YNP but within the RZ (OutYNP). Bears living inside YNP had lower survival (0.485 and 0.721, respectively), and bears living outside the RZ (OutRZ) had the lowest survival rates (0.101 and 0.354, respectively).

Eight candidate models with $\Delta \text{QAIC}_c < 2$ included 1 or more of the following covariates: (1) OutYNP and OutRZ, (2) winter severity index, (3) index of population size, (4) litter size, (5) mother's age, and (6) median whitebark pine cone count. Seven of the top 8 models contained the OutYNP and OutRZ parameters (Tables 8 and 9). None of the top 8 models with $\Delta \text{QAIC}_c < 2$ and only 3 of 19 models with $\Delta \text{QAIC}_c < 4$ detected an effect of sample, suggesting that differences in survival of study sample versus conflict sample of bears was unimportant in the cub and yearling cohorts examined. This was confirmed by overlapping estimates of cub survival ($\bar{x}$, lower–upper 95% CI) for study sample (0.64, 0.39–0.82) and conflict sample (0.61, 0.29–0.86), and yearling survival for the study sample (0.90, 0.39–0.99) and conflict sample (0.54, 0.02–0.91). Although there was overlap in yearling survival estimates, mean survival was substantially different (0.90 vs. 0.54) between study and conflict samples. Our ability to detect a difference was likely due to the large sampling variance coupled with our small sample size.

In addition to OutYNP and OutRZ, several temporal and individual covariates appeared in the top models (Tables 8 and 9), including WSI, minimum population index, litter size, female age, and whitebark pine. Survival was positively affected by winter severity (Table 10). The more severe the winter, the higher the survival for both cubs and yearlings. During our study, winter severity ranged from -2.2 to 2.2, with a mean (± SE) of 0.4 (± 0.3). The 95% confidence interval for the β coefficient for WSI from our second-ranked model bounded 0, suggesting uncertainty in the predictive power of this covariate. Survival was inversely related to population size (Table 10). The index of population size ranged from 135 to 478, with a mean (± SE) of 256 (± 21.6). We fit both linear and quadratic models of female age. The quadratic model had a ΔQAIC_c of 3.20 compared to the linear fit of age that had a ΔQAIC_c of 1.53, indicating substantially more support for the linear model. Cubs and yearlings of older females survived at a rate higher than cubs of younger females (Table 10). The estimated β coefficient from the linear model was 0.194 (SE = 0.27, CI = -0.34–0.73). The 95% confidence interval overlapped 0, indicating a high degree of variation in the data set. Mean litter size for the sample we used to estimate survival was 2.3. Survival tended to be higher in years of good whitebark pine cone production (Table 10). Median cone production ranged from 0 to 29.

We attempted to estimate temporal process variance, defined as the inherent stochasticity of changes in the population level (White 2000), of cub and yearling survival rates (White et al. 2001, Burnham and White 2002) using annual survival estimates from the $s + t$ model (i.e., the samples (*s*) were sample- and conflict-trapped bears, and time (*t*) was additive). However, 6 of 17 estimates of cub annual survival and 13 of 17 yearling estimates were 1.0, with SE = 0. As a result, estimates of mean survival from the variance components model were much higher than observed survival rates. That is, estimates from the model that assumed constant survival across time gave a cub survival estimate of 0.62 (SE = 0.096, 95% CI = 0.42–0.79). The process variance model estimated mean cub survival of 0.87 with SE = 0.06, which conflicts with the data. Likewise, the mean estimate of survival for yearlings from the temporal process variance model was 1.0, again inconsistent with the observed estimates. We do not believe the process variance model realistically estimated mean survival because of the large number of survival estimates of 1.0 with SE = 0; we have no confidence in resulting estimates of process variance.

DISCUSSION

Our survival results show evidence of an interaction between density dependence and residency. The practical significance of this finding is that the relative importance of human-caused versus natural mortality apparently varies among different regions of the GYE. We expand on this findings here.

Our sample covariate did not appear in any of our best models, suggesting that management status did not influence survival of cubs and yearlings. This finding differs from previous research where management status affected survival rates of adult bears (Pease and Mattson 1999, Boyce et al. 2001, Haroldson et al. 2005*a*). Because we did not have telemetry collars on cubs or yearlings, we were unable to document cause of death in most cases. The exception was associated with the conflict sample, in which all cub deaths resulted from management actions.

Our analysis suggests that survival of cubs and yearlings is not independent of litter size. Offspring born to 1-cub litters died at a higher rate than those born in 2- or 3-cub litters. These findings agree with Craighead et al. (1995:196) that “survival increased with litter size increase” and Tait (1980) that abandonment of a single cub litter could improve a mother’s expected number of recruits to the population.

Residency of the adult female appeared in all top models (Table 8). Haroldson et al. (2005*a*) detected a relationship between residency of independent subadult and adult GYE grizzly bears and their survival rates. Survival of independent bears was highest in YNP, followed by OutYNP, and OutRZ. We found that cub and yearling survival was highest in OutYNP, followed by YNP, and lowest in OutRZ. Our findings are probably the result of an interaction between residency and increasing population density manifested as a density-dependent reduction in survival of young, which we expand on below.

Humans were responsible for >85% of documented mortalities of adult bears (Haroldson et al. 2005*a*). Deaths of about 1/3 of cubs and yearlings in our overall sample were human-caused, but the proportion of these mortalities as a percent of all mortality was not uniform. We documented 24 deaths of cubs or yearlings when residency InYNP was ≥50%, with 17% of these mortalities human-caused. When residency for OutYNP was ≥50%, we documented 9 deaths, of which 33% were human-caused. When residency for OutRZ ≥ 50%, we documented 9 deaths, of which 78% were human-caused (Fig. 10). Mean residency for the sample (alive and dead) was 0.454, 0.446, and 0.100 for InYNP, OutYNP, and OutRZ, respectively. The observed pattern of human-caused mortality as a proportion of total mortality was InYNP < OutYNP < OutRZ, which is identical to the one observed for independent bears (Haroldson et al. 2005*a*), suggesting that human-caused patterns of cub and yearling mortality were similar (Fig. 10).

The major difference we observed in the pattern of cub and yearling survival compared to adults was associated with higher rates of mortality for bears spending proportionally more time within YNP. Cause of nearly 83% of cub and yearling deaths was unresolved for bears spending the majority of their time InYNP, whereas only 11% of deaths were unresolved for bears spending the majority of their time OutRZ (Fig 10). Our mortality database (IGBST, unpublished data) suggests that when human-caused mortality is excluded, nearly all cub and yearling deaths where cause is known can be attributed to starvation and predation. Hence, mortalities associated with bears spending the majority of their time InYNP were heavily weighted by what likely represents natural mortalities, whereas mortality for individuals spending the majority of their time OutRZ were nearly all human-caused.

Our third model contained the covariate MinPop, and had strong support as an explanatory model, based on both $\Delta QAIC_c$ and $QAIC_c$ weights. The β coefficient for the MinPop covariate was negative, suggesting that survival declined as population size increased (although the confidence interval bounded zero). This result suggested that we were observing density-dependent mechanisms in survival (see Schwartz et al. 2005*b*, Fig. 4 for an argument that density increased during this study). Density was not uniform across the study area, and area occupied changed as well. During our study, counts of unduplicated females from the entire GYE steadily increased, whereas counts inside YNP remained relatively constant (Schwartz et al. 2005*b*, Fig. 5). We suggest that the population of bears inside YNP likely has reached carrying capacity, whereas the population outside YNP is still growing. Consequently, one would expect density-dependent effects in survival to manifest themselves first within YNP, and later in the expanding frontier of the population beyond the RZ. We observed this pattern, with natural mortality (presumed starvation and predation) as a proportion of total mortality contributing most within YNP. This pattern also suggests that natural mortality likely will increase as this population reaches higher densities outside YNP, assuming existing protections are sufficient to minimize or eliminate human-caused deaths.

Although we expect the rate of both natural and human-caused mortality to be influenced by density, we also recognize that human-caused mortality was probably not uniform among the 3 zones of residency. The IGBC recommended during the 1980s that state and federal agencies implement management actions (Knight et al. 1999, USFWS 2002) to improve grizzly bear survival inside the RZ, including YNP. These actions were undertaken as part of the Grizzly Bear Recovery Plan (USFWS 1993) and included managing garbage within YNP and adjacent communities, implementing backcountry food storage rules, and removing most sheep allotments on National Forest lands. These actions have not been implemented outside the RZ. The pattern of human-caused mortality we documented supports other assessments that these actions have been successful (Mattson 1990, Gunther 1994).

Our mean estimate of cub survival (0.83) when OutYNP was set to 1 was similar to the 0.87 documented in Noatak Preserve, Alaska (Ballard et al. 1991) and the 0.77 documented in the Swan Mountains of northwest Montana (Mace and Waller 1998). The estimate was slightly higher than those reported for hunted brown bear populations in the Susitna Basin (0.67) and Black Lake area of the Alaska Peninsula (0.57) (Miller et al. 2003). Our mean estimate of survival for cubs InYNP (0.48) was slightly higher than that reported for unhunted populations in Denali National Park (0.34) and Katmai National Park (0.34) (Miller et al. 2003). These comparisons also support our findings that the population within YNP is probably at or near carrying capacity, whereas the population beyond its borders is below carrying capacity.

Our models suggested cub and yearling survival improved following severe winters. Mattson (2000) found females that ate ungulate carcasses lost more cubs than females not using this food (Mattson 2000). Increased cub loss was attributed to conspecific killing due to increased exposure to other bears. We do not know the foraging behaviors of females in our sample. Additionally, Mattson (2000) did not contrast or discuss cub survival in his female sample following severe versus mild winters; he only contrasted survival of cubs for females using varying amounts of high-protein food. Although our results seem contrary, it is plausible that carcass abundance influences the likelihood of exposing newly emerged cubs to other bears, especially adult males. In years of abundant carcasses, there would be less competition for specific carcasses. Thus, one might anticipate a lower exposure rate and improved survival.

A mother's age has a positive effect on survival of dependent young. Primiparous females tend to lose litters more often than multiparous females (McLaughlin et al. 1994). Analyzing cub loss among individual female grizzly bears in the GYE, Mattson (2000) suggested that young and old females had a higher probability of losing a cub than prime-aged females. We detected lower survival associated with younger females, but not for older females; the oldest female in our sample successfully raised 2 cubs at age 22. Our observation that young females lose more offspring than older females interacts with our observation that single-cub litters die at a higher rate than multiple-cub litters because young females tended to produce smaller litters than prime-aged females (Schwartz et al. 2005*c*).

Survival improved with whitebark pine seed production. Cone production in the year of survival was in our top models. Whitebark pine seed production and grizzly bear survival are related in the GYE (Blanchard and Knight 1991, 1995; Mattson et al. 1992; Mattson 1998). High mortality occurs during poor seed crop years; in adult and independent subadults, this mortality is a result of increased killing of bears by humans (Haroldson et al. 2005*a*). For cubs and yearlings, the mechanisms are less clear because cause of death for most cubs and yearlings was undocumented. Management removal of adult females and their dependent young causes loss of offspring. Seven of 10 documented cub deaths occurred during the 4 years in which median whitebark pine cone production was zero. The other 3 were removed in 2001 from the southeast part of the GYE where records also indicated poor cone production (Haroldson and Podruzny 2002). Thus cub and yearling survival during years of poor cone production are influenced by their mother's survival.

On occasion, grizzly bears kill one another. Adult males have been implicated as the cause of death for cubs and yearlings in nearly 78% of cases where age and sex of killer was known (McLellan 1994). Cubs are the greatest victims. Two competing hypotheses are postulated on effects of intraspecific killing in bear populations (Miller 1990*b*). One suggests that greater mortality of adult bears will result in increased survival of young bears, particularly cubs. Although some studies have demonstrated a negative relationship between the recruitment of subadults and number of adult male bears (McCullough 1981), others (Miller 1990*a*, Garshelis 1994) caution against density-dependent interpretation until the effects of nutrition and other confounding factors can be distinguished. The second hypothesis proposes that conspecific killing of unrelated cubs by adult male bears may increase male fitness if the male doing the killing subsequently impregnates females that lose offspring (Hausfater and Hrdy 1984). The hypothesis predicts that survival of cubs would decline after a resident adult male was killed due to immigration of nonresident males (Swenson et al. 1997) or resident adult males that were not the cubs' father (Swenson 2003). To test this, we added temporal covariates of the number of adult (age >4 years old) or total number of male bears known to have died in the GYE the year prior to estimating survival of cubs to our intercept model. Neither covariate appeared in our best models and the results were ambiguous. The β coefficient for the all-male covariate was negative, whereas the coefficient for adult males was positive. A negative coefficient is consistent with sexually selective infanticide, because as male mortality increases, cub survival declines. However, the positive coefficient for adult male mortality supports the density dependence theory; as adult male mortality goes up, cub survival increases. Confidence intervals for both parameters bound 0, suggesting poor fits. Additionally, both hypotheses imply a spatially explicit relationship between male removal and survival. We made no effort to incorporate either into our models because we had no data on the area used by the males dying in the GYE.

MANAGEMENT IMPLICATIONS

The States of Idaho, Wyoming, and Montana have all identified areas of suitable grizzly bear habitat within the GYE beyond the RZ (USFWS 2002) where bears will be allowed to recolonize. For bears to reestablish in these areas, mortality must be balanced with reproduction. Because agencies can do little to influence reproductive output, they focus on managing mortality.

Our best models indicated that survival of dependent young was strongly related to where the adult female and her young lived in the GYE. Bears living outside the RZ had a much lower probability of survival. In cases where mortality could be documented, humans were the predominant cause of mortality. In suitable grizzly bear habitats, agencies should consider implementing management actions outside the RZ like those employed by the IGBC (USFWS 1993) to reduce mortality to include food and game meat storage regulations on public lands, garbage management in public campgrounds, and enhanced outreach efforts on private lands. We recommend expanding information and education programs directed at private landowners.

Our best models also suggest that population density may influence cub and yearling survival in the GYE. One implication of this finding is that we should anticipate reduced survival in the RZ outside YNP as density there reaches carrying capacity. Also, without additional mechanisms to reduce bear mortality outside the RZ, we anticipate increased mortality in this zone as bear density increases. However, if regulations similar to those in the RZ are implemented, we would anticipate improved survival that could approximate what we measured in the RZ, but which would eventually decline toward survival rates measured in YNP as population density reaches carrying capacity. Regardless, our models suggest that managers must recognize potential density-dependent effects and consider them in future modeling and decision making.

SURVIVAL OF INDEPENDENT GRIZZLY BEARS IN THE GREATER YELLOWSTONE ECOSYSTEM, 1983–2001

MARK A. HAROLDSON, CHARLES C. SCHWARTZ, AND GARY C. WHITE

Survival rates of adult females are critical demographic traits necessary to assess trends in large mammal populations. Recent analytical techniques applicable to radiotracking data allow for the investigation of individual and temporal covariates that may affect survival (White and Burnham 1999). These techniques apply maximum likelihood theory to estimate survival rates, use the information-theoretic method for model selection and multi-model inferences (Burnham and Anderson 2002), and estimate temporal process variance (Burnham and White 2002). Separating process from sampling variance is important when projecting biological populations (White 2000). Here, we estimate mean and process variance of annual survival rates and evaluate the effect of temporal and individual covariates on annual survival for independent (i.e., subadult ages 2–4 and adult ≥5 years old) grizzly bears in the GYE.

METHODS

Field Methods

Most methods used were presented in Schwartz et al. (2005*b*). Here, we detail specific methods to estimate survival of independent bears and model effects of temporal and individual covariates on survival.

Survival

Radiotracking records were converted into monthly encounter histories (White and Burnham 1999) for each bear in each year monitored. Availability began during month of capture and continued through the end of the year or until the bear was censored. We censored data from an individual beginning with the month immediately following its last location if time between telemetry locations exceeded 60 days during the active season (Apr–Oct). The median number of days between successive locations within a calendar year for all bears monitored was 7 (range 0–165). Median days between successive locations after censoring was 7 (range 1–60). We relaxed this 60-day rule during the period when most bears were denned (Nov–Mar). For bears entering dens, we required 1 location during November or December for these months to be included through the end of the year. For bears exiting dens with active transmitters, we considered January the starting month if we had locations during the primary denning period (Jan–Mar). If we did not acquire a telemetry location during the primary denning period, the month in which the animal was initially located became the first month available for that individual. We adopted these procedures because bears wearing functioning transmitters were occasionally lost once they entered winter dens, but were reacquired soon after emergence, and our data indicated bears rarely died in their dens. Bears that shed transmitters were right-censored (Pollock et al. 1989) to the month the last active signal was obtained. Deaths were assigned to the month when date was known or to month of the last active signal when exact date was unknown.

The fate of some instrumented bears was unknown. We classified fate as unexplained if radiotransmission ceased, the cessation could not be logically attributed to expected battery life (i.e., <24 months for 36-month transmitter), and the individual was never recaptured. Some bears initially classified this way were later found to have been illegally killed and their collars destroyed. Instances in which stationary transmitters were irretrievable due to logistical field constraints and the individual never recaptured were designated unresolved. We suspect that some of these were human-caused mortalities because we documented transmitters cut from bears that were intentionally discarded in log jams and off cliffs. However, natural mortality also might have occurred at these sites.

Factors Affecting Survival

Because fates for some radiocollared bears were unknown, we constructed 2 data sets for analysis reflecting alternate treatment of individuals. Bears classed as unexplained or unresolved losses were either: (1) right-censored to month an active transmitter was last located and considered censored (C) from the data set, or (2) assumed dead (AD). This approach yielded 2 datasets that essentially bounded survival estimates for the population (Heisey and Fuller 1985, Pollock et al. 1989).

We used the known fate data type in Program MARK (White and Burnham 1999) to estimate mean survival and its process variance and to investigate the influence of various covariates on survival. The known fate model employs binomial likelihood functions over a specified interval (monthly in our case) and allows consideration of individual and external covariates (White and Burnham 1999).

We separated estimates of process from sampling variance (White et al. 2001, Burnham and White 2002) using the variance components procedure available in Program MARK. The analysis was complicated by high survival rates, particularly among adult females. Estimates of annual survival were near 1 or occasionally equaled 1, resulting in estimated SE = 0. As a result, estimates of process variance and accompanying sampling variance were biased. To circumvent bias, process variance was estimated from parameter estimates based on the logit model. Annual survival was estimated as

$$\hat{S}_i = \frac{1}{1 + \exp(-\hat{\beta}_i)},$$

and the process variance of $\hat{\beta}$ values was estimated and back-transformed to the scale of the survival estimates. We estimated annual survival in Program MARK to use for calculation of process variance with a model that used a 1/12-time interval (0.08333333), a year effect for 19 years as a categorical variable (allowing each year to have a unique survival estimate), with additive sex and sample (study or conflict) effects. Process variance and mean survival were computed for only study sample bears, although the additive effect of the conflict sample affected estimates of study sample bears. Because the sex effect in the model was additive on the logit scale, temporal process variance of males and females was the same on the logit scale, although the standard deviation of shrinkage estimates ($\tilde{S}$, White et al. 2001; i.e., survival estimates that have been shrunken by excluding variation attributable to random effects and including only process variation) was different for the sexes. Sample sizes were inadequate to estimate male and female process variance independently. Estimates of mean survival and process standard deviation were computed for both the C and AD data sets. The SD of the annual survival (back transformed $\bar{S}$ values) is an estimate of total SD on the real scale.

We investigated the influence of individual and temporal covariates on survival using an a priori set of 42 candidate models developed from various combinations of covariates (see Schwartz et al. 2005*b*). Structure for all a priori models was additive, with no interaction terms. We ran duplicate model sets with the C and AD data sets. We used the design matrix feature of Program MARK with a logit link to constrain models (White and Burnham 1999). Our input specifications consisted of 38 groups (i.e., 19 years study sample and 19 years conflict sample), 12 occasions (i.e., months), and 6 individual covariates. Individual covariates included sex, age class, presence of dependent young, prior management history, sample category, and residency. Temporal covariates included year, month, season, and indices of winter severity, annual whitebark pine cone abundance, ungulate biomass, and population size (Schwartz et al. 2005*b*, Table 1). Individual and temporal covariates were identified, and a priori models developed in part based on Pease and Mattson (1999) and Boyce et al. (2001).

RESULTS

During 1983–2001, 323 grizzly bears were radiomonitored for 5,989 bear-months. Numbers of individuals monitored annually increased (Fig. 11), ranging from a low of 17 in 1985 to a high of 84 in 2001. Numbers of females monitored annually also increased (Fig. 11), averaging 15 (range 4–28) and 8 (range 3–15) females/year for study sample and conflict sample, respectively. Peak numbers of bears monitored (i.e., 1984, 1988, 1994–1996, 2001; Fig. 11) occurred during or the year following poor food production. During such years, bears moved more in search of food, were more vulnerable to baited traps, and were prone to conflict. These conditions generally resulted in more study and more conflict captures. Months of availability also increased annually through the study period (Fig. 11). Average number of months monitored per individual varied by group, sex, and age class (Table 11). In general, adults were monitored longer than subadults, females longer than males, and bears from the study sample longer than those from the conflict sample (Table 11).

Two hundred and twenty-five bears were part of the study sample at some point, of which 201 (81 F, 120 M) were first tagged by researchers. Of these 201, 6.9% (7 F, 7 M) were censored and subsequently recaptured at management trap sites and entered the conflict sample. Sixteen bears (11 F, 5 M) were captured at management trap sites while being monitored as part of the study sample and did not change their status under our protocol. Nine bears (4 F, 5 M) initially monitored in the study sample had management captures either before 1983 or while they were dependent offspring.

A total of 122 bears (50 F, 72 M) were initially captured at management trap sites and monitored under the conflict sample. Of these, 24 (19.7%; 9 F, 15 M) were later captured at research sites and became part of the study sample. Overall, of the 225 (201 + 24) bears monitored as part of the study sample, 28% (F = 34.4%, M = 23.7%) were involved in management actions at some point during or prior to the study; and 16.9% (F = 17.8%, M = 15.6%) also were included in the conflict sample. Of the 4,181 bear-months that study sample bears were monitored, 20.0% (F = 22.2%, M = 17.3%) involved bears that had prior management captures.

We documented 69 mortalities of instrumented bears (Table 11), averaging 3.6 bears/year. No known losses occurred in 1991 (Fig. 12*a*), but we documented ≥1 known mortality in all other years, with a maximum of 11 occurring during 2001. Female losses averaged 1.4 bears/year (study sample $\bar{x}$ = 0.4, range 0–2, conflict sample $\bar{x}$ = 1.0, range 0–3). We also observed an increasing trend in number of known mortalities outside the RZ during recent years (Fig. 12*a*). Only 5 (7.2%) known mortalities, all adult males, were attributed to natural causes: 2 from maladies associated with old age, 2 from conspecific predation, and 1 undetermined. Specific cause of death could not be determined for 5 (7.2%) documented mortalities. Most known deaths (n = 59, 85.5%) were caused by humans, including 35 (59.3%) sanctioned management removals, 12 (20.3%) killed by hunters in pursuit of game or in hunting camps, 11 (18.6%) poaching or malicious killings, and 1 (1.7%) accidental electrocution from a downed power line. Twenty-six and 43 of the 69 known mortalities were part of the study sample and conflict sample, respectively (Table 11). Nineteen mortalities from the study sample were human-caused, and 5 (2 F, 3 M) of these were management removals. Forty bear deaths from the conflict sample were human-caused, and 27 (11 female, 16 male) of these were management removals.

We identified 22 additional unexplained or unresolved losses (Table 11) during 12 of the 19 years ($\bar{x}$ = 1.2 bears/year, range 0–5; Fig. 12*a*). Ten of the unexplained or unresolved losses were female bears ($\bar{x}$ = 0.5 bears/year, range 0–3; Table 11) with most (68.2%) from the study sample (9 female, 6 male).

Most mortality occurred during August–October (Fig. 12*b*). All documented natural mortality occurred during April or May. Known deaths from undetermined causes were distributed throughout the active season. We documented 3 mortalities during November–December (considered part of the hibernation season in our models), but all were of bears that had not yet entered dens. A strong correlation existed between the number of unexplained or unresolved loss and known human-caused mortality expressed on a per month basis (Pearson's r = 0.74, P = 0.004). Both of these loss categories were highly correlated with monthly sample size (Pearson's $r > 0.84$, $P < 0.001$), which also peaked during the autumn.

Mean Survival and Process Variance

Using the C and AD data sets, the 1/12-time interval input specification, and an $S_{(t)}$ model constrained by study sample and sex, our estimate of mean survival during 1983–2001 was $\bar{S}_{C\,M}$ = 0.874 (95% CI = 0.810–0.920) and $\bar{S}_{C\,F}$ = 0.950 (95% CI = 0.898–0.976) for males and females, respectively (Table 12). Estimates of survival using the AD data set were $\bar{S}_{AD\,M}$ = 0.823 (95% CI = 0.746–0.880) and $\bar{S}_{AD\,F}$ = 0.922 (95% CI = 0.857–0.959) for males and females, respectively. Estimates of process standard deviation on the logit scale were 0.279 (95% CI = 0–0.856) and 0.442 (95% CI = 0–0.977) for the C and AD data sets, respectively (Table 12).

Average annual estimates of survival and shrinkage estimates of annual survival (White et al. 2001) for both data sets were computed as the logistic transformation of the annual $\hat{\beta}_i$ s and the shrunk $\hat{\beta}_i$ s (Table 13). Estimates of the process SD on the real scale were 0.0304 and 0.0134 for males and females, respectively, for the C data set and 0.0661 and 0.0343 for males and females, respectively, for the AD data set (Table 13).

Influence of Temporal and Individual Covariates on Survival Estimates

In general, identical models built with the 2 alternative data sets (censoring unknown fates, or assuming those animals had died) were ranked similarly. Models with year as a covariate, however, were consistently better (i.e., smaller ΔAIC_c) in analyses using the AD data set. This result can be explained because some portion of the unexplained or unresolved loss was likely due to malfunctioning radios and hence added losses uncorrelated with any explanatory variables. Consequently, other temporal covariates explained less annual variation when these losses were included as dead bears. For this reason we restrict our results in the remainder of this section to those obtained using the censored data set.

Six of the 42 candidate models had $\Delta \text{AIC}_c < 2$ (Table 14), indicating similar support for these models (Anderson and Burnham 1999). These 6 models also accounted for 73% of AIC_c weights among candidates considered. Covariates common to all were sample, sex, season, whitebark pine (WBP), and residency (OutYNP and OutRZ). These covariates also ranked high in importance (Table 15) when we summed AIC_c weights of models containing them over the entire set of candidate models (Burnham and Anderson 2002). Covariates influenced survival in the directions expected (i.e., sign of the $\hat{\beta}_i$ s was consistent with a reasonable biological interpretation, Table 16), with 95% confidence intervals that did not include zero (except OutYNP) and were the covariate set in the top model (Table 14). Results from these models indicate that survival of grizzly bears was influenced by: (1) sex, females had higher survival rates than males; (2) sample, bears monitored under the conflict sample had lower survival than study sample bears; (3) residency (OutYNP and OutRZ), survival decreased as bears spent more time outside the RZ (Fig. 13); (4) season, bears had highest survival during hibernation, followed by spring–summer, with lowest during autumn (Fig. 14); and (5) WBP, bears had higher survival during years with good cone production, especially individuals in the conflict sample (Fig. 15).

Other covariates appeared in the 6 best models, but had relatively low rank and β coefficient with 95% confidence intervals that overlapped zero. These included WSI, UngBio, AgeC, and DepYng. Two of the 6 best models used the top 6 covariates plus 1 additional covariate (second best model included WSI, fourth best model included UngBio; Table 14) and as such, these models (and covariates) were probably not strongly supported (Burnham and Anderson 2002:131). The other 3 models with $\Delta \text{AIC}_c < 2$ contained 2 additional covariates (third best WSI + AgeC; fifth best WSI + DepYng; sixth best WSI + UngBio; Table 14) and also were likely influenced by presence of the top 6 covariates. Covariates not present in models with $\Delta \text{AIC}_c < 2$ and with 95% confidence intervals that overlapped zero in all models were Prior, MinPop, Year, and Month. We suspect that prior management status did not appear in our top models because the covariate sample (study sample vs. conflict sample) was a better predictor of survival. When both variables were included in the model, Prior had no impact. The finding that Year and MinPop were not important suggests that survival was fairly constant and was not influenced by changes in population size, which increased during the study (Fig. 3 and 4)

DISCUSSION

To our knowledge, the duration of monitoring and the sample sizes that we report are the largest for a single study addressing grizzly bear demographics in North America (McLellan et al. 1999, Schwartz et al. 2003*a*). This large sample combined with a detailed understanding of food habits, movement patterns, and causes of mortality allowed us to build our suite of a priori models that help explain the dynamic nature of grizzly bear survival in the GYE.

Although we divided our data into 2 samples based upon circumstance of capture, inclusion of all information in models provided a better understanding of effects of individual and temporal covariates on survival. We estimated that our study sample and conflict sample were approximately 12 and 6%, respectively, of the minimum population estimate derived from counts of unduplicated females. These values represent maxima because our index of population size is a minimum, not a true estimate. If we consider distinct families (Knight et al. 1995) summed over 3 years as a minimum estimate of adult females in the population, then on average, we monitored 18 and 8% of the adult females annually under study and conflict settings, respectively.

The way we grouped our data was a key consideration when attempting to estimate grizzly bear survival in the GYE in an unbiased manner (Schwartz et al. 2005*b*). When estimating adult female survival, Eberhardt (1995) used only individuals initially captured at research trap sites, recognizing that some of these bears might later be captured in management actions. Eberhardt (1995:15) asserted that, “although management activities are a major cause of mortalities, only a relatively small fraction of adult females are at risk from such activities any given year.” He estimated that <3% of the adult female population was managed annually and concluded that his method produced representative estimates of survival. Pease and Mattson (1999) considered that bears captured near major developments were, or would become, nuisance bears, and additionally that offspring of nuisance bears acquired their mother’s status. Following this rationale, they concluded that 73% of the individuals in the population were problem bears and projected that the population was greatly influenced by lower survival rate of managed bears.

Using our methodology, 28% of all study sample bears were involved in conflicts before or during the study. Of the female bears in our study sample, 34.4% were involved in conflicts. From the perspective of the monthly sampling unit, 20.0% of all study-sample bear-months involved bears with prior management captures, and 22.1% of study-sample female bear-months involved bears with prior management captures. We conclude that our estimates of survival derived from our study sample represent the population at large. Survival estimates for bears monitored as part of the conflict sample do not represent the population at large but rather a group of individuals at high risk. However, because we incorporated information from the conflict sample into our models, these individuals contributed to our understanding of the influences of individual and temporal covariates on survival.

Our analyses used 2 data sets that differed in their assumptions regarding unresolved losses. Consequently, our estimates of survival essentially bound the range as determined by imprecision and error (Pollock et al. 1989). Because the C data set included only known mortalities, average survival estimates can be viewed as an upper bound to survival. And because the AD data set included known mortalities plus unexplained or unresolved losses counted as deaths, estimates of survival derived from these data are probably low because some individuals considered to have died probably did not. Previous authors (Eberhardt et al. 1994, Eberhardt 1995, Boyce et al. 2001) typically censored unexplained and unresolved losses unless circumstances supported a possible death. The correlation between known human-caused mortalities and unexplained or unresolved losses per month, adjusted for monthly sample size, supports the notion of human involvement in a portion of these losses. Finally, we may have underestimated survival because we assigned month of death as the last month the individual was known to be active when a bear was lost from monitoring and the date of death was unknown. If some of these individuals were lost the following month, our overall estimate of survival would be slightly low.

As in other studies (McLellan et al. 1999, Johnson et al. 2004), humans were the primary agent of grizzly bear deaths in the GYE. Eighty-five percent of known losses were directly attributable to human causes. We believe that most known losses from undetermined cause and the unexplained or unresolved losses also were human-related. The fact that we rarely documented natural mortality (5 of 64 deaths [7.8%] where cause was known) for grizzly bears past the age of dependency was probably due to 2 factors: (1) natural mortality agents are rare once grizzly bears reach adulthood (Eberhardt 2002); and (2) human-caused deaths are likely partially compensatory to natural mortality. Reported natural deaths of independent grizzly bears in the literature were caused mainly by accidents, conspecific predation, and occasionally by old age (McLellan 1994, McLellan et al. 1999). Our findings were similar. Few bears likely have the opportunity to die of old age in the GYE outside YNP. Subadults and senescent bears in poor condition typically get into trouble with humans in their search for food, especially during autumn, and are removed by managers before they die of natural causes. These situations are usually exacerbated during years with poor natural foods.

Our best estimates of female (C = 0.950, AD = 0.922) and male (C = 0.874, AD = 0.823) survival from our study sample for the GYE population from 1983–2001 are similar to survival rates reported for grizzly bears in southern Canada and the continental United States north of the GYE (McLellan et al. 1999). Our estimates of female survival also are similar to those of Eberhardt (1995) for adult GYE females (0.943) during 1983–1994. Eberhardt (1990) similarly concluded that a female survival rate >0.90 is needed to sustain the population.

Our best models suggest that several individual and temporal covariates influenced survival of grizzly bears in the GYE. The most important were sample, sex, season, OutYNP, OutRZ, and WBP. Female survival was higher than that of males, which is consistent with other analyses of brown bear survival rates in North America (McLellan et al. 1999, Schwartz et al. 2003*a*). Most natural deaths occurred in spring, whereas most human-caused mortalities occurred in autumn. Because nearly all the mortalities were human-caused, our models appropriately predicted survival was lowest during autumn (when conflicts between bears and humans are highest, Gunther et al. 2004).

Our models indicate a spatial component to bear survival. Bears living outside the RZ had lower survival than those living inside the RZ and YNP. The strong negative effect of OutRZ on survival, together with the increased proportion of instrumented bears located outside the RZ in recent years (Fig. 16), seemed incongruous with relatively constant survival through the study period. To investigate this apparent contradiction, we added Trend (through years 1–19) as an additional covariate to our previous best model (Table 14) in an a posteriori analysis. This new model (WBP + Season + Sample + Sex + OutYNP + OutRZ + Trend) clearly improved the previous top model (Table 14). The β coefficient for Trend (Table 15) indicated a significantly positive change in survival from 1983–2001. This trend was offset in recent years by the lower survival rate associated with an increasing number of bears outside the RZ in our sample. This result suggests a source–sink process for grizzly bears in the GYE, which Schwartz et al. (2005*d*) discuss in detail. The fact that we observed higher bear survival with time inside the RZ, both within YNP and outside YNP when accounting for likely environmental covariates, suggests that management actions implemented by the IGBC have been effective (Mattson 1990, Gunther 1994).

The relationship between poor whitebark pine cone production and increased bear mortality has been well documented (Mattson et al. 1992, Blanchard and Knight 1995, Mattson 1998), and our results provide additional support. Analyzing GYE grizzly bear mortalities, Mattson (1998) concluded that the decline in deaths through time was due to increased whitebark pine seed production during 1989–1992 rather than IGBC management actions. Mattson (1998:135) concluded, “there is little support for the assumption that management intervention caused declines in recorded mortalities.” His analysis was based on counts of dead bears, counts of radiocollared bears, time, and whitebark pine seed crops. Our analysis estimated survival rates in a spatial context, accounting for whitebark pine seed crop and trends in survival. Although our results do not prove this, they strongly suggest that management intervention initiated in the early 1980s was effective or that circumstances for bear survival inside the RZ were different from outside it, independent of IGBC actions.

Our best models (Table 15; $\Delta\mathrm{AIC}_c < 2$) and accompanying β coefficients (Table 16) can be used to estimate monthly survival. For example, to estimate survival in June (season = spring–summer) for a female bear (sex = 1) that is part of the study sample (sample = 0) in YNP (OutYNP = 0, OutRZ = 0), we can use the βs for the best model (Table 16):

$$\hat{S} = \frac{1}{1 + \exp(-(3.93 + 0.75 + 1.05))} = 0.997$$

Because there are 4 months in this season, this estimate must be raised to the fourth power, yielding an estimated seasonal survival rate of 0.987.

Covariates DepYng, UngBio, WSI, AgeC, Prior, and MinPop were not significantly related to survival of independent bears. Our findings regarding dependent young are contrary to those of Boyce et al. (2001), who reported lower survival in females accompanied by young compared to lone females in the GYE. The discrepancy likely reflects (1) different years, (2) the way individuals were categorized into samples, or (3) the way females with young were classed. Boyce et al. (2001) estimated survival during 1975–94, whereas we examined 1983–2001. We started with 1983 because it represents the approximate nadir in grizzly bear numbers in the GYE following listing and corresponds to the time when management actions to improve bear survival were implemented by the IGBC (see Schwartz et al. 2005*b*). Boyce et al. (2001) also followed the sampling protocol of Eberhardt et al. (1994) and classified individuals as research or management bears based on location of first capture. Finally, Boyce et al. (2001) classified females with 2-year-olds as accompanied by young but did not indicate if this status changed within a given year. We only considered females with cubs and yearlings as accompanied by young, because typically females wean 2-year-olds in spring and are alone for the remainder of the year. The discrepancy between their results and ours is likely due to a combination of these items.

Ungulates are an important food item for grizzly bears in the GYE (Green et al. 1997, Mattson 1997*a*, Jacoby et al. 1999) probably more so during years with poor whitebark pine seed production (Felicetti et al. 2003). The finding that UngBio and WSI were not important covariates in our models does not diminish the importance of ungulate meat to bears, but rather suggests that yearly variability in our indices of meat availability was not associated with adult survival. Our index of ungulate biomass did not vary greatly during the study period (Table 2), compared to changes during the decade following cessation of ungulate reduction programs (Yellowstone National Park 1997). Inclusion of these indices in the suite of covariates may have value for future investigations, given possible future scenarios for ungulates in the GYE in the presence of wolves, chronic wasting disease (Williams and Young 1980, 1982; Gross and Miller 2001), management of brucellosis (*Brucella abortus*), and threats to whitebark pine (Reinhart et al. 2001).

We did not detect a difference in survival between subadult (age 2–4 yr) and adult bears (age >4 yr). McLellan et al. (1999) found similar rates of survival and no difference between subadult (2–5 yr) and adult (>5 yr) female grizzly bears in the interior Rocky Mountains of Canada and the northern United States (Montana, Washington, and Idaho). Our results are not directly comparable to those of Eberhardt et al. (1994) and Eberhardt (1995) from the GYE because they considered subadults as bears aged 1–4 years and adults >4 years old and pooled data due to limited sample size. Also, their age categories included both dependent (i.e., yearlings) and independent (i.e., 2–4 yr old) bears.

We considered survival of dependent offspring separately using different techniques (Schwartz et al. 2005*a*). Age class appeared as a covariate in our third best model (Tables 14 and 16), but had a 95% confidence interval that overlapped zero. Estimates of subadult (0.945) and adult female (0.960) survival from this model (Table 16, model 3) were not biologically different from our estimate of female survival (0.958), excluding this age class distinction with other covariates held constant (Table 16, model 1). A review of the literature on estimates of female survival (Schwartz et al. 2003*a*:Table 26.5) suggests that subadult versus adult rates can be similar, lower, or higher depending upon area. Hence, our single estimate of survival for all females past the age of dependency is biologically defensible and simplifies population modeling (Harris et al. 2005).

Prior, which was a binomial covariate indicating previous management of each individual each year, did not appear in our top models. Intuitively, prior conflict should have influenced survival estimate. Boyce et al. (2001) demonstrated an increased risk of mortality with number of translocations (problem bears moved from a conflict site) for individuals, but their sample only considered bears initially trapped at research sites and not bears initially targeted as management problems.

Our dissatisfaction with covariate Prior not appearing in top models led us to another a posteriori modeling exercise in which we included 6 new covariates to explain acute and chronic effects of management. We coded a reverse trend during years that bears were involved in management actions. Thus, to assess a 3-year management effect (MgtEffect), bears were given MgtEffect3 = 3 during years they were involved in management actions, a 2 the next year (assuming no additional conflict), a 1 the following year, and 0 for ≥4 years following management. We used a similar procedure to code management effects 1–2 and 4–6. These covariates allowed us to identify the duration of management effects on bear survival by comparing AIC_c values of models that included MgtEffect1–6. Further, including MgtEffect1 with any of the other MgtEffect covariates allowed us to model both acute and then chronic effects. We used our original top model (Table 14) and substituted MgtEffect covariates for Sample, and combinations of MgtEffect1 with MgtEffect2–6 for Sample (Table 14). The new top model (WBP + Season + MgtEffect2 + Sex + OutYNP + OutRZ) was 19 ΔAIC_c units better than the original top model from our a priori candidate set. Results suggest that if managed bears did not come into conflict with humans for at least 2 years, survival was similar to bears with no known history of conflict (Fig. 17). Our analysis suggests a substantial decrease in survival during year of conflict from 0.95 to 0.71, with a chronic effect the year after a conflict (0.88), but with little if any effect 2 years later. This result is contrary to the life-long reduction of survival used by Pease and Mattson (1999) to characterize bears with a history of conflict.

Life-history theory (Eberhardt 1977; Fowler 1981, 1987; Gaillard et al. 1998; Eberhardt 2002) suggests a sequence of changes in vital rates occurs as population density increases toward a maximum. This sequence is: (1) increased mortality in immatures; (2) increased age of first reproduction; (3) reduced reproduction; and (4) increased adult mortality. The variable MinPop did not appear in our best models, suggesting no evidence of density-dependent effects on survival of independent (aged ≥2 yr) bears. Schwartz et al. (2005*a*, *c*) report evidence of density-dependent effects on reproductive output, and to a lesser extent, on cub and yearling survival in the GYE.

MANAGEMENT IMPLICATIONS

Our results demonstrate the value of long-term telemetry studies when attempting to understand how environmental and individual covariates affect survival rates in a threatened grizzly bear population. Significant loss of whitebark pine due to blister rust (Reinhart et al. 2001) or mountain pine beetle (*Dendroctonus ponderosae*; Haroldson et al. 2003) would reduce survival rates for bears, especially conflict-prone individuals. Should whitebark pine decline rapidly, we speculate we would witness a scenario similar to what occurred when dumps were closed in YNP; more management problems, particularly outside the RZ, with a substantial increase in measurable bear mortality.

Should loss of whitebark pine occur as a slow, chronic decline, we may not readily detect possible changes in survival rates in the short term without a very large sample size. In either case, the effects likely will be better documented and understood by maintaining adequate annual samples of radiomarked bears in the GYE.

Finally, our results demonstrate that humans are the single greatest cause of grizzly bear deaths in the GYE. Bears that come into conflict with people have a higher probability of dying the year of conflict, but if they remain trouble-free for ≥2 years, their survival rate returns to that of unmanaged bears. These results have important implications for management. First they demonstrate that managers should continue and expand efforts to minimize conflict situations (i.e., removal of garbage) and maintain a high rate of survival within the GYE. They also suggest that if conflicts can be minimized or eliminated, problem bears will have the benefit of a higher rate of survival. Efforts to minimize conflicts between people and bears represent a major component of any management program directed at the long-term conservation of the GYE grizzlies. Without such efforts, the proportion of problem bears in the GYE will increase, overall survival will decrease, and population trajectory will change.

TRAJECTORY OF THE YELLOWSTONE GRIZZLY BEAR POPULATION UNDER ALTERNATIVE SURVIVAL RATES

RICHARD B. HARRIS, CHARLES C. SCHWARTZ, MARK A. HAROLDSON, AND GARY C. WHITE

The grizzly bear population inhabiting the GYE is of national and international interest. Although this population has increased in size and extent in recent years (Eberhardt et al. 1994, Eberhardt 1995, Boyce et al. 2001, Schwartz et al. 2002), isolation from other grizzly bear populations and continuing human development along its geographic margins justify continued concern about its future.

Since the adoption of the federal Recovery Plan for grizzly bears in the United States (USFWS 1993), mortality of grizzlies in the GYE has been monitored and a standard for acceptable mortality limit established. One important component of the limits of acceptable mortality is an estimate of the maximum human-caused mortality sustainable by a grizzly bear population (Harris 1986). This level was generated for a generic bear population, but recent information specific to the GYE population now allows for improvements to this estimate. Here, we use data from 1983–2002 (Haroldson et al. 2005*a*, Schwartz et al. 2005*a*, *c*) as the basis for deterministic calculations and short-term stochastic projections of the GYE grizzly bear population under a range of survival rates for independent females (i.e., those no longer under the care of their mothers) that might apply in the future.

Our approach to stochastic simulations was to produce a series of basic projections using parsimonious interpretations of data from Schwartz et al. (2005*a*, *c*) and Haroldson et al. (2005*a*). We faced a number of different ways to project populations and interpret results, and we considered them as alternatives explored through sensitivity analyses. In generating trajectories, we wished to estimate not only the expected (or most likely) outcome, but also the probability of decline (because declines are possible even when expected $\lambda > 1$). Thus, we emphasized appropriate treatment of yearly variability in vital rates. Although analyses by Schwartz et al. (2005*a*, c) and Haroldson et al. (2005*a*) identified strongly supported environmental covariates, these failed to explain the full range of yearly variation in vital rates. A mechanistic model that simulated these environmental factors directly (and linked vital rates to them) would have yielded less yearly variation than was observed during 1983–2002. We therefore integrated all factors contributing to yearly variation (both identified and unknown) via our estimates of the true process variance (yearly variation of the population only, excluding sampling variation).

Because our objective was to understand survival rates that minimized the risk that λ would decline below 1.0, we focused on females. However, male mortality rates are relevant to more general conservation concerns, so we also examined the behavior of simulated populations under alternative male survival schedules. We claim no ability to predict future reproductive or survival rates as environmental or management factors change. We can, however, use our knowledge of patterns in vital rates from 1983–2002 to understand population trajectories associated with a range of plausible future vital rates.

METHODS

Deterministic Estimation of λ and Elasticity

We used the life table and matrix projection modules of PopTools (G. M. Hood, 2004. PopTools version 2.6.2. http://www.cse.csiro.au/poptools) to calculate deterministic (and therefore approximate) estimates of λ and elasticities (Benton and Grant 1999, de Kroon et al. 2000). To generate elasticities, we first used PopTools to transform reproductive rates (summarized by m_x) to the F_x values required for a Leslie matrix (see Taylor and Carley 1988). Reproductive (m_x) rates were set throughout at 0.318 (Schwartz et al. 2005*c*). We produced 2 alternative survival schedules, roughly corresponding to the 2 possible independent female survival rates of Haroldson et al. (2005*a*). As in the stochastic simulations, we adjusted cub and yearling survival rates from their mean estimates to account for the assumption that cubs and yearlings died if their mother died.

Data Sources and Parameterization

Data on reproductive parameters (Schwartz et al. 2005*c*), survival of dependent offspring (Schwartz et al. 2005*a*), and survival rates and variances for independent bears (Haroldson et al. 2005*a*) were from the entire GYE (Schwartz et al. 2005*b*).

Reproductive Rates.—Schwartz et al. (2005*c*) reported mean litter size during 1983–2002 of 2.04 (SE = 0.06). Our simulation tool used a multinomial distribution to model litter sizes. We used probability of litter sizes of 0.176, 0.608, and 0.216 for litters of 1, 2, and 3 cubs, respectively (Schwartz et al. 2005*c*). The age-specific probability of breeding given that a female was not accompanied by young during the breeding season, followed Schwartz et al. (2005*c*).

Interval between births was incorporated in the stochastic simulations via the interaction of probabilities of female breeding, entire litter loss, and age of litter at weaning. Field data on age of weaning from the GYE were sparse and unreliable, so we adjusted age of weaning in the model until the resulting value of female cubs/female (age ≥4 yr)/year approximated 0.318 (Table 4; Schwartz et al. 2005*c*). This process allowed us to reproduce the actual structure of the breeding system in grizzlies (e.g., litters must first be weaned or lost before a female is receptive again), fix the simulation to the most robust data (litter size and proportion of females breeding by age), and closely approximate observed m_x (female cubs/female/year) despite the absence of reliable data on weaning. To confirm that intervals between births produced in our simulations were similar to field data, we ran a trial simulation for 50 years and tallied the frequency of intervals for every female having >1 litter. We used a constant function relating female age to reproductive performance.

Survival Rates.—We used mean survival rates of 0.640 for cubs and 0.817 for yearlings (Schwartz et al. 2005*a*). Mortalities of these dependent offspring included those assumed to have been lost when mothers with litters died (or were removed). We retained the assumption that cubs and yearlings would always die if their mother died, and thus used variable rather than constant survival rates for cubs and yearlings. To do this, we first adjusted cub and yearling survival rates to those that would have applied during 1983–2001 had maternal survival been 1.0 (i.e., 0.684 for cubs, 0.873 for yearlings). In stochastic simulations, cubs and yearlings were given a survival rate of zero if their mother died that year. This reproduced mean survival rates for cubs and yearlings at approximately the mean independent female survival rates observed during 1983–2001 (Haroldson et al. 2005*a*), but allowed them to vary proportionally with alternative values of independent female survival.

We considered the possibility that variation of male survival rates would influence cub survival (via sexually-selected infanticide, *sensu* Swenson et al. 1997; Swenson et al. 2001*a*, *b*). However, the confounding and equivocal relationships Schwartz et al. (2005*a*) reported between number of male mortalities and cub survival in the subsequent year provided us no firm basis to model any relationships between male mortality and dependent offspring survival.

Independent female survival was the main independent variable of interest, because we assumed that variation of cub and yearling survival (other than the dependence on mothers explained above) would largely be unaffected by future management decisions. Estimates of independent mean annual female survival during 1983–2001 in the GYE were 0.922 (treating all unresolved losses as mortalities) and 0.950 (treating all unresolved losses as censored at the time of last contact; Haroldson et al. 2005*a*). Here, we varied hypothetical survival rates from 0.87 to 0.95 in 0.01 increments, a range that included certain decline and certain increase.

Most previous analyses of grizzly bear demographics recognized 1 or more subadult age classes (the period after dependence on their mother but prior to full maturity; Knight and Eberhardt 1985, Eberhardt et al. 1994, Hovey and McLellan 1996, McLoughlin et al. 2003) with lower survival rates. In contrast, other grizzly bear studies documented subadult female survival higher or nearly identical to adult female survival (McLellan et al. 1999; Schwartz et al. 2003*a*:Table 26.6). Models of survival for grizzly bears in the GYE (Haroldson et al. 2005*a*) did not support delineation of a separate subadult age-class. Therefore, we used a relatively simple model containing cubs, yearlings, and all older animals (i.e., ≥2 yr old). We put no upper bound on longevity because we lacked data from the GYE to support parameterization of declining survival with age; individuals were retained in the model until they died.

Stochastic Projections of λ

Simulation Program.—All simulations were conducted using a computer program named Generalized Animal Population Projection System (GAPPS; Harris et al. 1986), a stochastic population projection tool that documented and recorded the life-history of each individual animal of each projection, and in which population statistics were built from user-defined groups of individuals. At each life-history stage, every animal was subjected to a Bernoulli trial at which the event (e.g., breeding, dying, becoming independent of mother) either occurred or did not according to probabilities we supplied. We assumed that each life-history event occurred just once each year (Fig. 18), similar to previous uses of this tool in analyses of grizzly bear demography (Harris et al. 1987, Harris and Metzgar 1987, Harris and Allendorf 1989, Mills et al. 1996). Thus demographic stochasticity was inherent in our projections.

Approach to Demographic Stochasticity.—Considerable confusion exists regarding the definition and appropriate approach to demographic stochasticity in projection models (Engen et al. 1998, Kendall 1998, Sæther et al. 1998, Brook 2000, White 2000). We view the stochasticity of concern to Kendall and Fox (2002) and Fox and Kendall (2002) as equivalent to what Conner and White (1999) termed "individual heterogeneity," in which differences exist among individuals (for genetic, geographic, perinatal, or other reasons) but are retained throughout their life. Except for the broad-scale spatial characteristics identified by Schwartz et al. (2005*c*) and Haroldson et al. (2005*a*), data available to us were insufficient to identify further sources of individual heterogeneity that may have characterized the GYE grizzly population during 1983–2002. Thus, we had no choice but to treat life-history rates of all animals within each class (sex, age, family-group status) as arising from a single distribution (which was, however, allowed to vary annually, see below). In contrast, our approach toward demographic stochasticity was more akin to standard frequentist statistics, or what White (2000) labeled "penny-flipping variation." That is, we viewed the GYE grizzly bear population during 1983–2002 as a single sample from a theoretically infinite universe of possible GYE grizzly bear populations that could have been produced from the same underlying complex of processes. This approach seemed appropriate because our objective was to project these bears into an unknown future in which their fates might vary from those observed during 1983–2002 given the exact same underlying processes. Thus, in our projections, demographic stochasticity (and hence variability of population trajectory) varied inversely with population size.

Simulation Run.—For each series of simulations (except those examining male survival, see below), we projected 15 years but recorded data for only the last 10. By ignoring the first 5 years, and thereby allowing age-structures from an initial population of 244 females (which had previously been built using an approximate, grizzly-bear like survival schedule) to fluctuate, we ensured some measure of independence among projections produced under identical mean rates. We selected 10 years as an appropriate compromise between a longer-time series (during which our projection would become increasingly unrealistic because density, geographic area, and other environmental factors affecting the population would undoubtedly change) and a shorter-time series (which would provide insufficient time for the true underlying dynamic to overwhelm yearly variance in any run). For all analyses except those considering effects of male removals, population trajectory was quantified by λ, the antilog of the slope of $\ln(N)$ (where N = abundance of all females) on time. To quantify effects of varying annual male (age ≥ 2 yr) survival, we calculated the distribution of minimum total population sizes during the first 6 years of each run resulting from each combination of male and female survival rates. We summarized results using means as well as lower 5% and 95% bounds for each set of simulations (under the dual rationales that 2.5% and 97.5% bounds would have had higher standard errors than 5% and 95% bounds, and that conservation interest is focused on the lower bound and thus a 1-tailed error rate of 5% may be of greater interest than 2.5%; Keating et al. 2002).

Treatment of Variance and Parameter Uncertainty

In recent years, numerous authors (Link and Nichols 1994, Gould and Nichols 1998, White 2000) have discussed the need to separate sampling from process variance when projecting population growth rates. Because raw yearly survival rates were high (in 1991, the naïve estimate of survival was 1.00), Haroldson et al. (2005*a*) first estimated annual survival rates on the logit scale $\hat{S}_i = \frac{1}{1+\exp(-\hat{\beta}_i)}$, which is bounded at 1.0, and later back-transformed them to the real scale. They then estimated process variance of the β_i using Program MARK (White et al. 2001, see also Burnham and White 2002). We used the shrinkage estimates (Morris 1983, Burnham and White 2002) of annual survival rate (Fig. 19) as the basis for assessing the appropriate frequency distribution of those rates to incorporate into stochastic simulations. We used 2 estimates of the process standard deviation of independent female annual survival in our basic projections: one associated with the censored data set of Haroldson et al. (2005*a*), which we termed “low” process variation, and the other estimate from data assuming all unresolved losses represented deaths, which we termed “high” process variation. To model annual variation, we first generated random normal deviates on the logit scale, with mean μ_β and standard deviation σ_β, and then back-transformed these to the real scale (Table 17). To avoid the bias caused by Jensen’s inequality (Karlin and Taylor 1976), we further altered the input values on the logit scale until the back-transformed mean survival of each simulation series was within 0.0005 of the desired value (e.g., we used a simulation intended to test a mean survival of 0.94 if the achieved mean was >0.9395 and <0.9405). In most cases, differences between intended and achieved mean survival were <0.0001. We did not model yearly correlation among reproductive parameters, cub survival, yearling survival, or independent female survival.

Sensitivity Analyses

Calculation of λ.—We considered 3 calculations of our summary statistic λ of population trajectory of simulated populations: (1) the antilog of *r*, where *r* was calculated as the least-squares regression slope of ln(females) on time; (2) the geometric mean of the 9 ratios of females in 10 successive years ($\lambda = [n_{10}/n_1]^{(1/9)}$); and (3) the arithmetic mean of the 9 ratios of females in 10 successive years ($\lambda = \sum_{i=1}^{9} \frac{n_{i+1}}{n_i} / 9$). We also tallied the number of years within each series of 10 that declines from the previous year occurred, allowing assessment of the predictive capability of any single yearly decline on the 10-year probability.

Initial Age-structures.—To examine whether a 5-year mixing period was sufficient to generate independent (and approximately stable) starting age distributions, we produced a set of projections with independent female survival of 0.89 in which we recorded the final 10 years of 30-year projections. We assumed that 20 years would be sufficient to guarantee independence and stabilization of a single initial age-structure. We chose a female survival of 0.89 because we knew that mean λ would be close to unity, and therefore that population sizes at year 30 would not vary widely from the initial number. Comparison among projections with much smaller or larger population sizes would have been confounded by the additional influence of varying demographic stochasticity.

Initial Population Size.—We knew that demographic stochasticity alone could theoretically affect population trajectory and that magnitude of demographic stochasticity is a function of population size. Because we lacked clear guidance on the best initial population to begin our simulations, we conducted an additional series of projections using alternate starting populations ranging from 13 to 539 females. This allowed us to examine whether our results were highly contingent on the size of our initial population. In all cases, we restricted these simulations to vital rates we knew (from previous work) would produce $\lambda \cong 1.0$, so that simulated populations would remain near their initial sizes throughout the 15 years of the simulation.

Age-specific Reproductive Function.—Schwartz et al. (2005*c*) found a weak, albeit significant positive relationship between litter size and mother's age (older females were more likely than younger females to produce a 3-cub litter). Similarly, Schwartz et al. (2005*a*) noted a positive relation between offspring survival rate and mother's age. Finally, Schwartz et al. (2003*b*), using data from a number of brown bear populations worldwide, demonstrated that reproductive senescence characterizes older-aged female grizzlies. Thus, we were concerned that a constant function relating fecundity (and cub survival) to female age would ignore secondary but possibly important effects of varying female age-structures. Therefore, we performed additional simulations on an alternative fecundity schedule of female age that incorporated both increasing fecundity (Schwartz et al. 2005*c*) and cub survival (Schwartz et al. 2005*a*) with maturity and decreasing fecundity with senescence (Schwartz et al. 2003*b*; Fig. 20).

Process Variation in Offspring Survival.—Schwartz et al. (2005*a*) were unable to separate sampling from process variation in offspring survival. We were concerned that projecting cub and yearling survival with only the annual variability arising from demographic stochasticity would bias our projections, particularly because we suspected that offspring survival truly did vary annually more than survival of older, independent animals (Gaillard et al. 1998, 2000). Thus we performed separate projections with cub and yearling survival subject to much higher annual standard deviations than in basic projections. As in simulating yearly process variation for independent females, we drew random normal variates of cub and yearling survival independently, with means and estimated process standard deviations on the logit (β) scale. These logit-scale values were then back-transformed to the real scale for application in the projections, with adjustment made to ensure the approximately correct mean and 90% coverage of survival. Sampling correlation between cub and yearling survival (Schwartz et al. 2005*a*) was estimated as -0.014 and was therefore ignored in bootstrapping (i.e., cub and yearling survival rates were generated independently in each simulated year).

Sampling Error.—Finally, we recognized that all life-history rates estimated from the GYE population during 1983–2002 were accompanied by sampling error. Although sampling error does not affect population trajectory per se and thus was appropriately removed from our basic projections, we were concerned that ignoring sampling variance entirely would encourage readers to impute more certainty to our projections than would likely be the case in their actual use. It would clearly be inappropriate to estimate population trajectories based solely on point estimates of survival and fecundity in the face of sampling uncertainty. Thus, we produced additional series of projections in which sampling variance was deliberately mixed back in with process variance (although at the level of the iteration, not the year within the iteration). To do this, we allowed each life-history rate to vary independently at each iteration, according to its mean and standard deviation (taken from the sources listed above). In the case of process variation for independent females, σ was itself only an estimate (and its 95% confidence interval overlapped zero, Table 17). Thus, prior to each iteration, we drew a random variate from the distribution of σ, given its estimated mean and standard deviation, and took that variate as the process standard deviation to apply to each yearly survival rate during that iteration.

RESULTS

Deterministic Estimation of λ and Elasticity

With independent female survival set at 0.95, independent female survival rates had a summed elasticity of 0.733. In contrast, elasticity of cub survival, yearling survival, and the summed reproductive contribution parameters (i.e., F_x) were each 0.089. That is, a unit change in independent survival produced over 8 times as much unit change in λ as the same proportional unit change in the other parameters. These life-history rates produced an expected λ of 1.076. The pattern of elasticities was similar with lower (0.92) female survival, but λ was reduced to 1.042 (Table 18).

Using independent female survival rates with bears that had unresolved fates censored, hypothetical populations living entirely within the 3 zones inYNP, outYNP, and outRZ had λ of 1.054, 1.121, and 0.887, respectively. When bears with unresolved fates were assumed to have died, λ for the 3 zones was 1.019, 1.088, and 0.898, respectively. Despite the higher elasticity of independent survival rates, these geographic patterns in λ were largely driven by the dramatic differences in offspring survival rates among the 3 zones (Schwartz et al. 2005*c*).

Stochastic Projections of λ

Realized versus Intended Life History Rates.—Simulations produced reproductive rates similar to those that characterized the GYE grizzly bears during 1983–2002 (Schwartz et al. 2005*c*), with mean cubs/female aged ≥4 years old/year of 0.635 (compared with 0.636 from field data calculated in the same way). The mean of completed inter-birth intervals produced by the interaction of litter age at weaning and litter production rate for unaccompanied adult females was 2.94 (SE = 1.157, *n* = 1,535). The proportion of inter-birth intervals comprising 1, 2, 3, 4, 5, and ≥6 years old was 0.08, 0.28, 0.40, 0.16, 0.06, and 0.03, respectively. Inter-birth intervals of 1 year occurred (despite no weaning of cubs in the simulations) when cub litters were lost entirely, allowing mothers to breed in successive years. Relatively long inter-birth intervals occurred (despite all litters being weaned by their second year in simulations) because adult females unaccompanied by cubs were assigned breeding probabilities of only 0.636 (Schwartz et al. 2005*a*), and thus some adult females failed to produce litters despite having already weaned their previous one. We were concerned that unrealistically long inter-birth intervals might be produced in the simulations because breeding probability was considered independent each year (whereas in nature, we suspect that healthy females are more likely to breed with each successive year of being unburdened by cubs). The low frequency of long inter-birth intervals (9% >4 years) suggested that upward bias in length of inter-birth intervals in the simulations was relatively minor. Mean age at first reproduction in simulations was 5.90 years, similar to the estimate of 5.81 years from field data (Schwartz et al. 2005*c*). Realized reproductive rates did not vary appreciably as other parameters were altered, so are not reported for other analyses.

Simulations satisfactorily produced survival rates we intended to model, with standard deviations affected both by modeled process variance and magnitude of demographic stochasticity (Table 19). Standard deviations varied inversely with independent female survival because demographic stochasticity was more influential in smaller populations than larger populations (Table 19). Modeled process variation produced distributions of yearly survival similar to those seen during the 1983–2001 period (Fig. 21).

Trajectories under Alternative Survival Rates.—Mean trajectories produced by stochastic simulations were only slightly lower than those suggested by the deterministic analyses (Table 20). Mean λ of the GYE grizzly bear population varied from 0.983 (under mean independent female survival of 0.87 and low process variance) to 1.074 (under mean independent female survival of 0.95). With low process variance, the lower 5% bound of simulated λ values was >1.0 (i.e., ≤5% of simulations declined over 10 years) when mean independent female survival was ≥0.90. With high process variance, a mean independent female survival of 0.91 was required before <5% of simulations declined (Table 20). Distributions of projected λ values were more variable with high process variance than low and with high demographic stochasticity (i.e., lower population size) than low (Fig. 22).

The probability of λ < 1.0 as a function of mean independent female survival was not linear, increasing abruptly as survival declined from 0.90 to 0.87 (Fig. 23). Projections with high process variance had higher probability of λ < 1.0 than those with low process variance at survival rates ≥0.89, but the reverse was true at survival rates of ≤0.88. This crossover resulted from the generally wider distributions of independent survival (and hence λ) under high process variation. Simulations with low process variation were more similar to the deterministic situation, in which probability of decline is a simple step function (i.e., 0 if expected λ is >1, 1 if λ <1), and thus displayed a more compressed sigmoid shape.

Alternative Male Survival Rates.—Projected λ values were unaffected by the survival rate of males in simulated populations. Altering male survival rates had the effect of changing the magnitude of truncation of the male age structure, but had no effect on female abundance or on λ during years 6–15. When male survival rates were applied that produced male age distributions more truncated than the initial age distribution, short-term (<8 years) declines in male abundance occurred, after which male abundance changed at the same rate as female abundance. Short-term reductions in total (male + female) abundance (i.e., prior to male age distributions stabilizing and male abundance changing at rate λ) relative to initial abundance varied from approximately 10 to 20%, depending on both female and male survival schedules (Fig. 24). No short-term reductions occurred when male survival was modeled as greater than female survival and female survival was >0.92, but male survival was unlikely to have been this high (Haroldson et al. 2005*a*).

Sensitivity Analyses

Calculation of λ from Simulation Runs.—All 3 methods of calculating population rate of change returned generally similar values (Table 21). The mean and standard deviation of λ returned by the geometric mean and regression approaches were almost indistinguishable (Table 21). Rates of population change suggested by the arithmetic mean of simple population ratios in successive years were biased high.

Period for Assessing Trajectories.—Longer periods allowed for more reliable estimates of the underlying trajectory of modeled populations than did shorter periods. Even assuming no sampling error, the probability of observing a population decline between any pair of years was a poor predictor of the 10-year trajectory of the population (Table 22). For example, a population growing at a mean annual rate of 4% had only a 1% chance of declining over a 10-year period, but >16% of yearly censuses showed declines from the previous year. In contrast, a population declining at a mean annual rate of 1.8% had >78% chance of declining over a 10-year period, but >44% of yearly censuses showed an increase over the previous year.

Influence of the Initial Age-structure.—When we allowed the age-structure of the population used to initiate all simulations to equilibrate for 20 years rather than 5 as in the main projections, with mean independent female survival of 0.89 and low variance, results were almost indistinguishable from those originally obtained. As in the basic projections, realized independent female survival (n = 3,000 iterations) was 0.890 (with 90% of 10-year runs returning means of between 0.851 and 0.927, compared with 0.848 and 0.935 in the basic projections) and realized mean λ was 1.006 (with 90% of values between 0.990 and 1.022; compared with 0.989 and 1.022 in the basic projections). The probability of decline over 10 years was 0.256 (compared with 0.261 in the basic projections, Fig. 23). The slightly more condensed distributions of survival rates and λ estimates were most likely caused by a slight dampening of demographic stochasticity associated with higher population sizes resulting from the longer equilibration period (20 vs. 5 yr, $\bar{x}$ of 270.8 vs. 246.3 females over the 10-yr period of projection) and not from any characteristics of the initial starting population. These results were sufficient to assure us that nothing in the single initial age-structure (at least as scrambled over a 5-yr pre-monitoring period) was sufficiently unusual or biased to affect the results of interest.

Demographic Stochasticity and Initial Population Size.—Mean λ was unaffected by the sizes of the starting populations we modeled (Fig. 25). Probability distributions of λ showed little change among initial population sizes of >100 females, but became more variable (i.e., distribution tails became wider) at initial population sizes of <100. All projections in our main results began from an initial population containing 244 females. It appears that the magnitude of demographic stochasticity inherent in projecting a finite population of this size is similar to that which would have resulted from beginning with initial populations of one-half, or double that size.

Alternative Age-specific Reproduction and Cub Survival.—The effects of ignoring increases in cub production and survival probability with age of the mother appeared to be approximately balanced by the effects of ignoring reproductive senescence at older age. Per capita female-only reproductive rates (m_x) under the alternative age-specific function (Fig. 20) were similar to the 0.318 obtained using the flat reproductive function (0.3178 when independent female survival was 0.87; 0.3175 when independent female survival was 0.95). Unsurprisingly, both mean λ and the probability of a decline were within 1% of the values obtained using the constant reproductive function. Thus we had no cause to conduct additional simulations with the more complex, age-specific fecundity schedule.

Process Variation in Dependent Offspring Survival.— Data were inadequate to allow Schwartz et al. (2005*a*) to separate process from sampling variance for cub and yearling survival. Yet we believed it likely that yearly variation in cub and yearling survival was greater than variation in survival of older animals (Gaillard et al. 1998, 2000; Eberhardt 2002). However, when we increased process variation in both cub and yearling survival, we produced little effect on λ (Table 23). Standard deviations roughly double those in the basic projections produced only a 0.001–0.002 increase in the standard deviation of λ. Although these larger standard deviations of cub and yearling survival do not appear high at first glance, they produced 95% confidence intervals greater than those observed in the GYE during 1983–2001 (Schwartz et al. 2005*a*), which included both process and sampling variation. Schwartz et al. (2005*a*) estimated mean cub survival as 0.640 (95% CI = 0.443–0.783), whereas under our increased process variance scenario, the 95% CI for cub survival was 0.383–0.778 when independent female survival was 0.87, and 0.454–0.806 when independent female survival was 0.95. For yearling survival, our increased process variance produced 95% CIs of 0.484–0.936 and 0.571–0.955 under independent female survival of 0.87 and 0.95, respectively, comparable to those Schwartz et al. (2005*a*) reported for yearling survival (0.489–0.944). Schwartz et al. (2005*a*) were handicapped by relatively low sample sizes in estimating cub and yearling survival during 1983–2001; thus, we suspect the variances associated with their estimates contained considerable sampling variation.

Accounting for Sampling Variance.—In contrast to the effects of increasing variability in cub and yearling survival rates, λ was sensitive to uncertainty about true independent female survival. Simulations in which expected independent female survival of 0.92 was allowed to vary across iterations with magnitude similar to the total (i.e., process and sampling) variance had a similar mean λ to those using only the mean survival rates, but SD_λ was over 4 times higher (0.068 vs. 0.015). As a result, the probability of decline over 10 years jumped dramatically from 1 to 23% (Table 24). Similarly, simulations in which expected female survival of 0.95 varied with SD = 0.029 showed no change in mean λ, but SD_λ more than tripled. The probability of a decline rose from <0.001 (none of 3,000 simulations) in the basic projections to about 3%.

DISCUSSION

As is true of any analysis, our interpretations and conclusions are only valid to the degree that sampled bears represented the entire population. Trapping efforts during 1983–2002 were intended to provide a study sample unbiased with regard to location within the ecosystem and based on analyses presented by Schwartz et al. (2005*b*), we believe this to be the case. However, as discussed by Schwartz et al. (2005*b*), a rigorously defined random sample was logistically and biologically impossible, and even with stratification of our sample there is still a possibility that small biases remained. But like every other study with grizzly bears, we cannot quantify the extent or even the direction of any such bias. We do not, however, believe that these minor biases, if they exist, alter the biological conclusions we have reached.

Elasticity analyses confirmed the importance of survival and relative unimportance of reproductive rates in contributing to λ, in accord with similar analyses (Taylor et al. 1987, Eberhardt et al. 1994, Hovey and McLellan 1996, Boyce et al. 2001). Unlike most previous analyses, we did not identify a separate subadult age class (Haroldson et al. 2005*a*), and thus elasticity for our independent females is higher than for 'adults' (usually ≥5 years old) in these previous analyses. Although adult survival typically exerts the most influence on population growth rate, subadult survival may respond most flexibly to changing environmental conditions (Gaillard et al. 1998, 2000; Eberhardt 2002).

Because neither reproductive rates nor survival of cubs was modeled as a function of male:female ratios, male survival and therefore male population size had no effect on λ, and reductions in overall abundance caused by increasing male mortality were short-term. This appears contrary to the suggestion of Swenson et al. (1997) that loss of adult males would reduce cub survival (and hence λ), but unlike their work, we had no basis for modeling a relation between mortality rates of adult males and cubs. Our modeling approach made no definitive statements about whether sexually-selected infanticide existed in the GYE grizzly bear population, but it did suggest that the magnitude of its impact on cub survival was unlikely to change measurably as a consequence of varying adult male survival.

Our stochastic models appeared to incorporate approximately the correct amount of annual variability in rates, as estimated during 1983–2002. This magnitude of annual variability was too low to substantially alter trajectories resulting from simple, deterministic life-table analyses. The primary benefits of performing the stochastic simulations were that they also provided estimates of the probability of decline even when expected λ was positive. Additionally, had we not incorporated the known variability of survival rates, we would have had no way of knowing that, in the final analysis, they had so little effect on expected λ.

As with any thorough analysis of a population, the best available data (Haroldson et al. 2005*a*; Schwartz et al. 2005*a*, *c*) left us with many uncertainties. We lacked certainty about the size and age-structure of initial populations from which to initiate stochastic projections. Runs with a much longer scrambling period suggested that results were not highly dependent on any particular initial age-structure. Similarly, we were reassured that the amount of demographic stochasticity we incorporated in the simulations was appropriate for a population roughly the size of the GYE population in year 2003 (the point of departure for projections; Fig. 25).

For simplification, our basic projections used a constant function relating cub production and survival to mother's age when we knew (Schwartz et al. 2005*a*, *c*) that, in fact, the true function was complex, peaking at ages when females were fully mature physically and had enough experience to effectively protect their cubs, yet were not so old that reproductive senescence had begun. However, our alternative reproductive-by-age schedule yielded very similar population trajectories to our simpler one, suggesting that the more parsimonious function cost us very little information.

Prior to performing all the calculations, we were not sure of the most appropriate way to summarize the trajectory of simulated populations. Our finding that regressing ln(*N*) on time yielded similar results to using the geometric mean suggested that, theory notwithstanding, it made little difference in this case. Finally, committed as we were to separating process from sampling variation, we were unable to satisfactorily estimate process variation for cub and yearling survival. Once again, however, our sensitivity analysis using the highest variance possible, given the 1983–2002 data, confirmed the elasticity result that yearly variation in offspring survival had little effect on population trajectories.

We considered the possibility that we failed to capture the true bounds of process variation of independent female survival during 1983–2001, and thus inadvertently biased our main body of projections. The 2 estimates of process variation produced by Haroldson et al. (2005*a*) were themselves accompanied by error terms, and their 95% confidence limits were wide and included zero. Although we cannot be certain, we doubt that true process variation in independent survival was substantially higher or lower than our bounding values. Had all variance observed in 1983–2001 independent female survival been due to sampling error (i.e., if process variance had truly been zero), this would mean that all independent Yellowstone grizzly bears actually had identical survival rates during every year of the period. Although it is well established that prime-aged females of long-lived species display little variation in annual survival (Gaillard et al. 2000, Eberhardt 2002), it does not follow that we would expect none at all, particularly given documented fluctuations of environmental factors known to co-vary with survival (Mattson et al. 1992, Mattson 1998, Haroldson et al. 2005*a*). At the same time, we doubt that process variation was truly much greater than our high value. Had it been so, this would imply that female grizzly bear survival based on monitoring an average sample of 15–23 collared bears/year (the lower figure is bears monitored in a research setting, the upper figure includes bears monitored in a management setting; Haroldson et al. 2005*a*) provided estimates essentially free of sampling error, which seems unlikely.

Thus, we have little reason to doubt that these estimates of λ and population decline are accurate if survival rates of independent females can be known without error. Unfortunately, such survival rates will almost certainly be accompanied by error terms. Indeed, Haroldson et al. (2005*a*) had no choice but to produce 2 survival estimates because of uncertainty about the fate of some study females during 1983–2001. Fortunately, such error can be quantified, and biologists and managers can take this important component of uncertainty into account in future assessments of population change. To indicate how much this matters, our final sensitivity analysis projected the Yellowstone population under the combined influence of process and sampling variation. Uncertainty about true independent female survival produced a dramatic increase in the risk of a population decline even when the expectation, using the best estimate of survival, suggested an increase. We suggest that it is probably better to treat the 2 types of variation separately: this could be accomplished by using only trajectories from population projections in which sampling variation of survival was removed, and by acknowledging sampling uncertainty by considering projections made under a broad range of survival values given the data rather than just the point estimate of survival (White 2000).

Our estimate that the GYE grizzly bear population is likely to maintain a positive trajectory as long as survival of females (≥2 years old) remains above approximately 0.91 (i.e., 9% annual mortality) would seem, at first blush, to suggest a radical departure from current guidelines. For example, Harris (1986:273) recommended that "the proportion of the female segment of the population that can be removed annually…without causing chronic decline should not exceed 3% of the female segment." More recently, McLoughlin (2002:33) suggested that "most grizzly bear populations in North America can tolerate approximately 3% total annual kill before declines…accelerate to unsatisfactory levels." Careful reading, however, reveals that, beyond some minor differences in assumptions and procedures, the apparent increase in tolerable mortality we report here arises not from real discrepancies in models or parameter values but rather from different ways of expressing a similar underlying dynamic.

Comparing our results with those of Harris (1986) is important because current management guidelines in the Yellowstone Grizzly Bear RZ (USFWS 1993, 2002) adopt an annual mortality limit derived largely from that work. First, our approach here differed fundamentally in that the earlier work attempted to estimate the mortality level associated with sustainability indefinitely. That is, Harris (1986) used a model of grizzly bear population dynamics that was self-regulating. Thus, bear populations equilibrated (rather than grew exponentially) in the absence of killing by humans. Adding human-caused deaths to this model engaged compensatory responses that were assumed to characterize grizzly bear populations (although parameters used to build the responses were not based directly on data, but rather were interpolated from general principles). Here, our aims were more modest: to project short-term growth rates applied under a range of plausible survival rates, making no assumptions about density-dependent (or other possible) regulating mechanisms that must, no doubt, intercede to change those trajectories at some point. Second, Harris (1986) assumed that natural mortalities, although decreasing as hunting increased, would never be entirely substituted by human-caused mortality. That is, even at the population level producing the highest sustainable yield indefinitely, background levels of natural mortality would continue. Harris' (1986) objective was to estimate the maximum human-caused mortality rate that, when embedded into the assumed compensatory structure, equilibrated the population with its carrying capacity. Here, we declined to suppose any particular relationship between human- and non-human-caused mortalities (to say nothing of carrying capacity). Indeed, we had no data to do otherwise, given that not a single independent female mortality in the GYE attributable to non-human causes was documented during 1983–2001 (Haroldson et al. 2005*a*). Dependent young experienced natural mortality, but because cubs and yearlings were not collared, cause of death was undetermined in many cases (Schwartz et al. 2005*a*).

Thus, contrasting our results directly with the 3% sustainable mortality rate of females estimated by Harris (1986) is inappropriate. Harris (1986) also assigned survival rates to 3 subadult female classes (2, 3, and 4 years old) in addition to 3 adult age classes, complicating any attempt to compare the total mortality rate sustained by adult females in his model populations with those we report here. Fortunately, we were able to rehabilitate the Harris (1986) model for application here and develop a common currency for comparison with our results. We discovered that maximum hunting rates he found consistent with sustainability (i.e., 6.85 female kills/year from a population of 193.5

females, or 3.54% of the female component killed annually; Harris 1986:276) corresponded to an annual survival rate of all females (cubs through the oldest class) of 0.851 (SD = 0.035, n = 3,000 iterations). For comparison, our survival rates of all females (irrespective of age) consistent with low probability of decline were 0.847 (SD = 0.022, n = 3,000 iterations) when independent female survival was 0.91 (under low process variation) and 0.852 (SD = 0.077, n = 6,000) when independent female survival was 0.92 (under high process variation). Thus, although the approaches and presentation of results were quite divergent, overall female survival rates consistent with non-declining populations in both Harris (1986) and our present effort were almost identical.

McLoughlin (2002) reported that a simulated population modeled approximately on the GYE grizzly bear data through 1995 displayed a breakpoint (at which persistence probability declined rapidly with additional kills) at a mortality rate of about 2.8%. However, human-caused mortalities in his model were assumed additive to natural mortality, which was set at 4.9% for females aged ≥6 years and 11.4% for females 2–5 years old (McLoughlin 2002:Table 2.1). With approximately 30% of the female population in ages 2–5 years and 46% ≥6 years old (approximately the case if the population had achieved its stable age distribution prior to additional harvest), the mean natural mortality rate for females ≥2 years old would thus be approximately 6.4%. This, added to the 2.8% annual kill yields 9.2% total mortality of females ≥2 years old (i.e., annual survival of 0.908), which is again similar to our conclusion that λ will be ≥1 with high probability when annual female (≥2 years old) survival rates were approximately 0.90–0.91.

Eberhardt (1990) also provided a simple deterministic model relating grizzly bear life history rates to stable trajectories. Application of the mean survival rates from our simulations (Table 19) to his Eq. 1 (Eberhardt 1990:587) produced r =0 (i.e., λ = 1.0) with independent female (≥2 years old) survival of 0.898 and age of first reproduction set to 5 years, as well with as with independent female survival of 0.906 and age of first reproduction set to 6 years (GYE mean during 1983–2002 was 5.81 years, but Eberhardt's [1990] equation did not allow for fractional ages). Although abstract, his model further confirmed our estimates of female survival rates consistent with non-declining trajectories.

MANAGEMENT IMPLICATIONS

Our efforts here did not attempt to estimate sustainable mortality rates, at least as that term is generally understood (i.e., referring to the sum of the processes whereby populations become internally regulated). Our approach contrasts with Harris (1986) and is conceptually similar to those taken by Taylor et al. (1987) and Eberhardt (1990), albeit with the addition of variance components analysis and explicit inclusion of stochasticity. Managers should also consider that these projections do not consider whether all short-term (i.e., about 10-year) declines are biologically meaningful. Here, we simply generated trajectories, but a population whose fundamental dynamic is stable can decline in the short-term strictly because of random processes. The reverse is also true (i.e., year-to-year increases are possible in a population with a fundamentally declining trend). Thus we caution managers to interpret future trend information with our 10-year time frame in mind.

The current approach to grizzly bear management in the GYE is for management agencies to consider all forms of mortality, but to establish an annual limit only for human-caused mortality. We propose that rather than counting human-caused mortalities, management agencies should focus on survival rates irrespective of the cause of death. By counting all deaths, it becomes unnecessary to determine exactly how a bear died (which often requires subjective judgments). It also minimizes the importance of knowing the proportion of human-caused deaths not documented (e.g., Cherry et al. 2002). As long as an active monitoring program is in place (including radiotelemetry of a random sample of bears to update life-history rates as condition change), demographic analyses can augment counts of reproductively active females (Knight et al. 1995, Mattson 1997*b*, Keating et al. 2002) as an indicator of overall population health.

The reader should also be mindful that this analysis used mean values for the entire GYE population from all years 1983–2002. In fact, it appears that as the population expanded during this time, survival rates probably changed. It is unclear how much of this was due to possible density-dependent effects and how much was due to a larger proportion of the population residing in riskier areas, particularly on or near private lands (Boyce et al. 2001, Haroldson et al. 2005*a*, Schwartz et al. 2005*a*, *c*). Our results should be robust to geographic heterogeneity as long as survival rates of independent females (and of dependent offspring; Schwartz et al. 2005*a*) are unbiased estimates of the GYE grizzly population. However, care must be taken to ensure that future estimates of survival and reproductive rates are not biased as density, geographic characteristics, environmental characteristics (e.g., climate change or reduction of seeds from whitebark pine), or human pressures on the population or its habitat change. Managers should also consider management approaches that explicitly acknowledge the source–sink scenarios presented here and discussed by Schwartz et al. (2005*d*).

IMPACTS OF SPATIAL AND ENVIRONMENTAL HETEROGENEITY ON GRIZZLY BEAR DEMOGRAPHICS IN THE GREATER YELLOWSTONE ECOSYSTEM: A SOURCE–SINK DYNAMIC WITH MANAGEMENT CONSEQUENCES

CHARLES C. SCHWARTZ, RICHARD. B. HARRIS, AND MARK A. HAROLDSON

By necessity, grizzly bear demographic models have largely ignored spatial considerations (McLellan 1989, Eberhardt et al. 1994, Eberhardt 1995, Hovey and McLellan 1996). However, ignoring spatial heterogeneity is equivalent to assuming that individuals live in a homogeneous environment and that all members of the population experience the same environmental conditions at any point in time (Pulliam 1996). Knight et al. (1988) were probably the first to recognize the potential effect of habitat heterogeneity on grizzly bear survival and impacts of sink habitats on long-term conservation of the species (see also Doak 1995). These sinks, associated with human activity and development, represented locations where grizzly bears obtained anthropogenic foods and suffered high rates of mortality.

Schwartz et al. (2005*a*) and Haroldson et al. (2005*a*) demonstrated that simple spatial indices of residency were consistently important correlates of survival. To understand the implications of geographically heterogeneous survival, we explored life tables corresponding to hypothetical grizzly bear populations whose residency varied from living entirely within Yellowstone National Park (InYNP), to entirely outside of YNP but within the USFWS designated RZ (OutYNP), and beyond the borders of the RZ (OutRZ), using survival rates of the top models of dependent and independent bears (Haroldson et al. 2005*a*, Schwartz et al. 2005*a*). These 3 zones correspond to distinct management approaches, although they doubtless ignore finer-scale correlates of survival. We further explored consequences of these simulations and discuss them in the context of source–sink theory, deviations from the theory, and implications for management. Additionally, we incorporate significant temporal covariates into our models and explore impacts of temporal heterogeneity (food availability) on population demographics.

METHODS

To explore effects of temporal and spatial heterogeneity on grizzly bear demographics, we built an array of deterministic models using survival estimates from our best models. We used the life table module of PopTools (G. M. Hood 2004. PopTools version 2.6.2 http://www/cse.csiro.au/poptool) to deterministically estimate λ. We fixed reproductive (m_x) rate at 0.318 (Schwartz et al. 2005*c*) and assumed an equal sex ratio at birth. We set age of senescence for adult females to 29 years based on the meta-analysis by Schwartz et al. (2003*b*), where maximum decline in per capita litter production occurred at 28.3 years of age. For cub/yearling survival, we used Model 2, (Table 8), and β coefficients (Table 10) (Schwartz et al. 2005*a*) that contained our residency covariates (OutYNP and OutRZ), and WSI; models with both WSI and WBP were 7 or more AIC_c units below the best models. This suggested that WBP was not an important covariate, so it was taken as constant for cub and yearling survival. We used models of survival for independent bears created from the censored data set (Haroldson et al. 2005*a*). We used Model 2 (Table 14) and the β coefficients in Table 16 of Haroldson et al. (2005*a*) because this was the second highest ranking model and had the residency covariates and WSI and WBP covariates. This model also considered sex, season, and sample. We only considered females from the study sample only, and computed annual survival over the 3 seasons. Survival estimates for independent bears from this model probably overestimate true survival in the population because some individuals considered to be censored likely died, thus underestimating mortality. Because survival of independent bears contributed >73% of the elasticity to calculations of λ (Harris et al. 2005), and because we did not incorporate measures of variance into our models (Karlin and Taylor 1976, Boyce 1977) we caution the reader not to interpret our estimates of λ as absolute, but rather to consider them relative to one another. We varied WBP from 0 to 30 and WSI from -2.2 to 2.2, the ranges observed during the study. We varied the location of residency within the GYE. We did not incorporate demographic stochasticity into these models because we were concerned with evaluating relative impacts of these covariates on λ rather than issues of variance.

RESULTS

Our spatial covariate explained major differences in survival among the 3 areas of residency. When combined with estimates of reproduction, λ varied with OutYNP > InYNP > OutRZ (Fig. 26). Absolute λ for the GYE depended on the proportion of bears residing in each zone. We do not know the density of bears in each area, but the sizes were 8,992, 14,836, and 10,663 km^2 for InYNP, OutYNP, and OutRZ, respectively, assuming the total area of bear distribution for bears in the GYE was 34,491 km^2 (Schwartz et al. 2002). If bear density was equal within InYNP and OutYNP, there would be 1.65 bears outside for every bear inside YNP. If density was higher InYNP as suggested by our detection of density dependence (Schwartz et al. 2005*a*, *c*), this ratio would be lower. Assuming our sampling of independent bears approximated the distribution of bears living in the GYE, the proportions were 0.393, 0.472, and 0.135 for InYNP, OutYNP, and OutRZ, respectively. The ratio from this sample was 1.2 bears OutYNP:InYNP.

When holding WBP and WSI at their means, spatially explicit estimates of λ were 1.04, 1.12, and 0.88 for InYNP, OutYNP, and OutRZ, respectively. For comparison, setting the residency covariate to the mean of our telemetry sample (0.393, 0.472, and 0.135 for InYNP, OutYNP, and OutRZ, respectively) and holding WSI and WBP at their means yielded a generic estimate of λ = 1.08 for the GYE. Clearly, the greatest influence on λ was the proportion of time bears spent outside the RZ.

Indices of whitebark pine and winter severity both appeared in the top survival model for independent bears, but only WSI appeared in the model used to predict survival of dependent young. When these 2 temporal covariates were modeled in combination with our residency statistic (Fig. 27), certain generalities became apparent. First, the residency covariate appeared to have greatest impact on λ followed by WSI and WBP. Additionally, the effects of WSI and WBP varied with residency, with changes in abundance of these foods having the greatest effect on λ outside the RZ. The slope of the line for WSI was much steeper for OutRZ than InYNP or OutYNP (Fig. 27).

Additionally, separation between the minimum, mean, and maximum WBP was greater for OutRZ as opposed to InYNP and OutYNP, suggesting variation in WBP had a greater effect on λ outside the Recovery Zone. For example, λ changed by 0.10, 0.05, and 0.17 for InYNP, OutYNP, and OutRZ, respectively, from mildest to severest WSI indices (2.2 to -2.2), while holding WBP at its mean. Conversely, λ changed 0.01, 0.02, and 0.05 for InYNP, OutYNP, and OutRZ, respectively, when we changed the WBP index from 0 to 29 cones per tree while holding WSI constant at its mean. Changes in λ for the poorest food year (WBP = 0, WSI = 2.6) to the best food year (WBP = 29, WSI = -2.2) were 0.12, 0.07, and 0.22, for InYNP, OutYNP, and OutRZ, respectively.

DISCUSSION

We recognize that all our covariates are inextricably linked in a continuous time series and cannot be uncoupled. Consequently, any estimates of reproduction or survival that we generate across observed changes in a covariate are not independent of one another. Hence, setting whitebark pine abundance to zero and estimating future λ should be taken at face value and not assumed to predict demographic vigor in the absence of this food. We also recognize that it is impossible to predict the future with complete certainty for any wildlife species. We emphasize that our analyses focus on relative changes in λ associated with changes in covariates and should not be considered as absolute.

Our initial estimate of population trajectory for the GYE was derived for a single aggregated population (Harris et al. 2005), but our best models clearly show that the GYE grizzly bear population displays heterogeneity of survival on a broad geographic scale. Survival is further influenced by availability of both ungulate carcasses in spring and whitebark pine seeds in autumn. When incorporating the spatial component of residency category, we see substantially different trajectories (Fig. 26). These geographic differences imply a source–sink dynamic across the GYE, with positive growth rates in YNP and outside YNP within the RZ, but negative rates outside the RZ. Declines in λ are most severe outside the RZ when foods are less abundant (Fig. 27).

Blanchard and Knight (1991, 1995) and Mattson et al. (1992) concluded that during years of poor whitebark seed production, bears made greater use of areas near humans and came into conflict more often with humans. As a result, management problems and the number of management-trapped bears increased. The annual number of recorded grizzly bear deaths from 1976–1992 was strongly related to whitebark pine seed use (Mattson 1998). Recorded mortalities were 1.8–3.3 times greater during years when pine seeds were not intensively used. Nearly all bears in their analysis lived within the RZ (Fig. 2). These early works did not incorporate a spatial component into analyses. Our results support their findings, but indicate that decline in λ during good versus poor WPB years was -0.018, -0.022, and -0.050 for InYNP, OutYNP, and OutRZ, respectively, largely because survival of independent females contributed 73% of the elasticity associated with changes in λ. Using the best model (Haroldson et al. 2005*a*), reductions in survival of independent females from good (WBP = 29) to bad (WBP = 0) cone crops were 2.0, 2.5, and 6.3% for independent females with residency set to InYNP, OutYNP, and OutRZ, respectively. All 19 WBP transects used to estimate annual cone production were within the RZ, but it is likely that cone production outside the RZ would correlate with transect results (Weaver 2001). Also, the extent of WBP outside the RZ is incompletely mapped, but we do not expect that much occurs at lower elevation sites (Weaver 2001).

Although our spatial analysis does not prove cause and effect, our results strongly support the hypothesis that IGBC management efforts reduced bear mortality and increased the population's growth rate. This conclusion is further supported by the finding that changes in abundance of whitebark pine had the least impact on female survival and λ within YNP, followed by the area outside YNP but within the RZ. Of the 3 zones we studied, YNP has the strictest controls on human activities that directly or indirectly influence bear survival. These restrictions include strict gun control, highly regulated front- and back-country camping, garbage management, no livestock grazing, and regulated access to vehicles and hikers. Within the RZ outside YNP, access management is less restrictive and hunting is permitted, but controls exist over anthropogenic foods (garbage management, back-country food storage) and nearly all sheep grazing has been eliminated. None of these restrictions apply outside the RZ. Our models consider survival and changes in λ by residency zone, taking changes of food abundance into account.

Source–sink theory was formalized by Pulliam (1988), although the concept was introduced by Levene (1953). A source population is one in which births exceed deaths and emigration exceeds immigration. In sink populations, deaths exceed births and immigration exceeds emigration (Pulliam 1988). Sinks often are associated with substandard resources and, consequently survival is possible but reproduction, although feasible, is poor (Danielson 1992). Animals move from source to sink habitats either because of density-dependent competition or density-independent dispersal (Holt 1993). Delibes et al. (2001) proposed that habitat selection is a key factor underlying source–sink dynamics. When individuals avoid sink habitats, the sink does not depress the source population. However, when animals choose habitats in a maladaptive way (either because they cannot distinguish sink from source or because they prefer the sink), the overall population declines and may go extinct. Such mortality sinks, originally termed ecological traps (Dwernychuk and Boag 1972, Gates and Gysel 1978, Pulliam 1996), result in high mortality or breeding failure in otherwise good habitats where resources are abundant (Gaona et al. 1998). Schlaepfer et al. (2002) further distinguished between ecological and evolutionary traps. Evolutionary traps occur in situations where a sudden anthropogenic change in the environment causes an organism to make a decision that normally would be adaptive, but results in a maladaptive outcome. In ecological and evolutionary traps, the agent of decline is a mismatch between an organisms' behavioral or life history choices and the state of the environment.

Experimental (Gates and Gysel 1978, Gundersen et al. 2001) and simulation (Pulliam 1996) studies of source–sink dynamics have primarily focused on plants, birds, or small mammals where individuals reside year-round *either* in a source *or* a sink habitat, but not both. Most simulations addressing larger mammals assume individuals move from one state to another as a result of emigration and immigration, so that individuals reside exclusively in source or sink habitats. Using grizzly bears as an example in a source–sink model (Doak 1995) allowed bears to move between 2 populations living in good and bad habitats with movements regulated by population growth rates in the 2 types; but individuals lived either in good or poor habitat, not both. Doak (1995:1374) recognized the limitation of his model when he stated "the model presented here is best thought of as a cartoon of grizzly bear populations."

The assumption that individuals reside exclusively in either source or sink habitats is unrealistic for animals with large home ranges living in spatially and temporally heterogeneous environments. Grizzly bears, for example, may include both source and sink habitats within their annual or life range (Knight et al. 1988). Bears are attracted to sinks in a maladaptive way because of the presence of anthropogenic foods. Such areas represent evolutionary sinks, or sinks associated with blatant disturbance (Schlaepfer et al. 2002). However, because these areas are contained within individual home ranges, they represent sinks where probability of mortality is greater than elsewhere within home ranges. Consequently, survival for any given bear within the GYE population is a function of the number and size of sinks within their home range, as well as the amount of time spent in sinks. This dynamic is further complicated by availability of natural foods. In a spatial context, survival for a grizzly bear population can be viewed as a product of multiple survival probabilities, where survival is high for certain individuals in certain areas and low in others. Overall survival for an individual is determined by where it resides on this probability surface and the amount of time it spends at any location on the surface (its utilization distribution). Any such utilization distribution is itself dynamic, changing with season, food abundance, demographics, and other environmental factors.

The GYE is effectively an island with one bear population. Our models suggest that survival for grizzly bears beyond the RZ is low, with most mortality on or near private lands: for bears outside the RZ, $\lambda = 0.878$; elsewhere within the GYE $\lambda > 1$. This source–sink pattern is expected and consistent with findings on extinction rates and reserve sizes for large carnivores (Woodroffe and Ginsberg 1998). Areas outside reserves are population sinks because large carnivores are often limited by humans killing them, and most deaths occur beyond reserve boundaries. High mortality is expected when large carnivores expand beyond boundaries of protected habitat or where the reserve is small relative to an individual's home range. Where reserves are large relative to home ranges, many individuals can live entirely within the protected area and are buffered from human killing. When reserves are small relative to home ranges, animals cannot live entirely within the reserve boundary and must use habitats that are less secure outside of reserves, which can result in reduction or even extinction of the population. This is particularly true where human killing represents the greatest threat to demographic stability. When this occurs, the survival of individuals, and ultimately of the population, is determined by the ratio of secure to non-secure habitat within individual home ranges, the relative amount of time individuals spend in each, and their cumulative effect on survival. The critical element of this dynamic is to ensure that on average recruitment equals or exceeds mortality for the population as a whole, recognizing that high human-caused mortality beyond suitable and secure habitats is expected and may exceed recruitment in some years. Maintaining a balance between recruitment and mortality is the crux of large carnivore conservation generally (Woodroffe and Ginsberg 1998) and grizzly bear management in the GYE specifically.

To ensure a self-sustaining population, reserves must be of adequate shape and size, and fecundity must be high enough so that recruitment equals or exceeds mortality, including mortality beyond the protected area (Woodroffe and Ginsberg 1998). Conservation and management then become a balancing act directed at minimizing, or at least managing, mortality for the population, recognizing that the majority of deaths for independent-aged bears will occur at the interface between bear habitat and humans. This dynamic has significant ramifications for future management of the GYE grizzly bears. How humans choose to live and behave at the interface between developed areas and secure grizzly bear habitat will determine the extent to which bears expand beyond the existing Recovery Zone. Actions taken by the IGBC in the early 1980s seemingly improved grizzly bear survival inside the RZ. As bears expand beyond this zone (Schwartz et al. 2002), and as the states of Wyoming, Idaho, and Montana identify additional lands deemed socially acceptable and biologically suitable for grizzly bear occupancy (USFWS 2002), measures must be taken to ensure that mortality, particularly that associated with sink habitat, does not result in a population decline in source habitat.

Because over 98% of lands are publicly owned within the RZ (USFWS 2002), IGBC management actions implemented in the 1980s affected virtually all available grizzly bear habitats within the RZ. However, management of attractants on private lands is a continuing problem. Within the RZ, 20% (26 of 127) of all known and probable human-caused grizzly bear deaths during 1983–2002 occurred on private land (IGBST, unpublished data). In contrast, outside the RZ, 62% (28 of 45) occurred on private lands. Private land outside the RZ constitutes 23% of the total current grizzly bear distribution. Managing human-caused mortality on private lands will be more difficult than on public lands. If the public can learn to live compatibly with bears and to minimize food conditioning and resulting bear–human conflict, then losses of bears on private land can be accommodated by bear production within secure habitats. However, human behavior along the edge must be continuously managed to prevent excessive bear mortality if continued expansion of bears into suitable habitats outsize the RZ is to occur. Management agencies must therefore focus their activities toward improving human coexistence with and acceptance of grizzly bears at this interface. How agencies respond to bear–human conflicts will affect population health, and will determine how far bears expand their range outside the RZ. Agencies must focus not only on removing problem bears, but also on developing and implementing ways to manage bear–human conflicts. And although "it's easier to destroy a bear than to manage sources of bear–human conflict" (Eberhardt and Knight 1996:420), both are necessary to maintain public acceptance of grizzlies and ensure long-term persistence of the species. Consequently, actions and impacts of private land development and agency responsiveness in and adjacent to grizzly bear habitats to address bear–human conflicts on private lands will, to a large degree, determine continuing success of the recovery process.

Development pressure in the GYE will almost certainly increase (Clark et al. 1999, Hansen et al. 2002), and some private lands currently dedicated to ranching and agriculture will be converted to rural residential development (Hernandez 2004). New development will increase sources of human foods and attractants that will potentially amplify grizzly bear–human conflicts and ultimately bear mortality. Additionally, many people moving into these new developments are immigrants from other regions of the United States (Riebsame et al. 1997) who often lack the knowledge and skills necessary to live compatibly with grizzly bears, making continuous outreach efforts even more necessary.

Human acceptance of grizzly bears will strongly influence long-term persistence. Although we lack a nationwide study addressing human attitudes toward grizzly bears in the GYE, Wyoming Game and Fish contracted a public attitude survey toward grizzly bear management in Wyoming (Kruckenberg 2001). Results showed that a large majority (74%) of Wyoming residents feel that grizzly bears benefit Wyoming and are an important component of the ecosystem that they occupy. Opinions on efforts to increase bear numbers in Wyoming were about equally divided between those who favored (42%) and opposed (39%) such efforts. Those in favor felt grizzly bears hold an important place in the ecosystem (40%) and should be protected from extinction (31%). Those opposed felt grizzly bears were dangerous to humans (36%) and livestock (18%). Support for efforts to increase bear numbers improved from 42 to 61% when coupled with the idea that wildlife managers would be stationed locally to track bears, inform and educate people, and resolve conflicts.

MANAGEMENT CONSIDERATIONS

Changes in survival and reproduction among our 3 defined zones of residency were principally influenced by 3 factors: humans killing bears, changes in food abundance, and density dependent factors affecting reproduction and survival of dependent young. We believe that our results represent the best available estimates of the present conditions of the GYE grizzly population, but recognize that we can and should seek to improve and update our data and information, and to expand our scientific understanding. We suggest that discussions about specific management recommendations made in this monograph include all groups interested in the GYE grizzly bears.

Natural Foods Monitoring

Our results clearly show that whitebark pine and winter weakened ungulates affect survival of independent and dependent bears. However, as discussed by Schwartz et al. (2005*b*), we did not explore the significance of all known foods (e.g., cutworm moth and cutthroat trout) in our models because we lacked adequate information to do so. We know cutworm moths and cutthroat trout may influence reproduction and survival of a segment of the bear population in the GYE. To improve our understanding of the role of foods in GYE grizzly bear demographics, we recommend the following data be collected for future modeling efforts:

1. Continue to monitor WBP seed production on existing transects.
2. As bears expand into new habitats, add new WBP transects outside the RZ so that inferences about seed production can be made over the entire distribution of grizzly bears.
3. Develop a WBP health monitoring program to track changes in blister rust infestation and other pathogens across the ecosystem.
4. Monitor consumption rates of WBP by individual bears using newly developed isotopic techniques (Felicetti et al. 2003). Such monitoring will allow for constructing models where WBP consumption is treated as an individual, rather than temporal covariate.
5. Attempt to develop a cutworm moth monitoring program to quantify abundance and use.

6. Develop improved methods to monitor the abundance of spawning cutthroat trout on tributary streams of Yellowstone Lake.
7. Continue to monitor use of cutthroat trout by grizzly bears. Repeat fish consumption studies and estimate the numbers and sex of bears using the fish resource with DNA fingerprinting (Haroldson et al. 2005*b*) and mercury residue analysis (Felicetti et al. 2004).
8. Monitor consumption of meat by individual bears using stable isotope techniques (Hilderbrand et al. 1996). Such monitoring will allow for constructing models where meat consumption is treated as an individual rather than temporal covariate.

Population Monitoring

Simulations conducted by Harris et al. (2005) quantified and confirmed conventional wisdom that changes in λ are largely influenced by changes in survival of independent females (73% elasticity), which is principally driven by human-caused mortality. Managing human-caused mortality was a major goal established by IGBC in 1983, and results of our spatial analysis suggest success in this management effort.

We recommend the following to improve our ability to understand the GYE population:

1. Identify additional areas outside the RZ that will be designated as biologically suitable and socially acceptable habitats for grizzly bears in the GYE. The states of Idaho, Montana, and Wyoming have agreed to this in their management plans. These lands should be managed as biologically secure habitat. Biologically secure habitat in aggregate would be defined as lands where on average reproduction and survival rates result in $\lambda \geq 1$.
2. Maintain a representative sample of radiomarked individuals. As indicated by Harris et al. (2005) results should be robust to geographic heterogeneity as long as survival rates of dependent and independent females are unbiased estimates of the entire GYE grizzly population
3. Estimate trajectory for biologically secure habitat in aggregate at approximately 10-year intervals. Harris et al. (2005) showed that with survival of independent bears ≥ 0.91 and $m_x = 0.318$ or higher, then $\lambda \geq 1$ with approximately 95% probability. Assuming that survival of independent females remains at or near our current estimate of ≥ 0.92, survival can be estimated with SE ≤ 0.02 from a telemetry sample ≥ 185 bear years. Assuming we continue to meet the IGBC mandate to maintain a sample of at least 25 radiocollared adult females/year, we can estimate a population trajectory in biologically secure habitat approximately every 8 years.
4. Continue counts of unduplicated females with cubs in all occupied habitats.
5. Conduct a demographic review to consider alternative methods for determining mortality limits based on findings in this monograph and those of Cherry et al. (2002). This review must recognize that habitat carrying capacity may change and may ultimately be reached; when that occurs, an annual management goal of $\lambda > 1$ is unrealistic. We recommend exploring alternative mortality limits that consider counting all forms of mortality — not

just human-caused — in any revised demographic management system, setting different mortality limits for independent females and males, and exploring mechanisms for more liberal mortality limits outside areas designated as biologically secure habitat.

6. Develop more sophisticated source–sink models using covariates that might explain observed differences in mortality rates among the 3 politically defined residency zones. We recognize that our 3 zones are a rather simplistic approach to spatial analysis.
7. Explore habitat use and home range sizes of historically collared bears to better understand potential edge effects (White et al. 1982) associated with home range size and the geographic extent of the existing RZ.
8. Explore dispersal rates and distances within the GYE to better understand where bears killed in insecure habitats originate.
9. Explore the influence of the type of conflict on subsequent survival of individuals. Our a posteriori models demonstrated that survival of individuals improved with number of years elapsed since the conflict. We suspect that conflict type (i.e., livestock, human dwellings, etc.) also could influence the rate of survival.

CONCLUDING THOUGHTS

Our interpretation of the accumulated data of the past 20 years (aided by considerable analytical effort) is that the GYE grizzly bear population has increased in abundance and expanded its range. Nevertheless, the lower confidence bounds on λ remain <1. Thus, although we find the evidence overwhelming that an increase has occurred, we cannot entirely reject the possibility that sampling error has misled us.

One possible approach to this dilemma is to focus on the left-hand side of the probability distribution surrounding the estimated rate of increase and argue that it cannot yet be stated with certainty that the population has increased. According to this argument, it should be assumed that the population has not increased and it should continue to be managed as though it had declined, or at best remained stable. This approach may superficially appear to be consistent with an undisputed tenet of science, namely transparently disclosing all sources of uncertainty. That, in turn, would appear to be an outgrowth of the movement to apply the ‘precautionary principle’, to wildlife conservation, an appealing if controversial approach that has been applied largely to pollution, pesticides, and genetic engineering (Foster et al. 2000, Appell 2001). Although we sympathize with the objectives of those promoting such an approach, we find it lacking as a basis for good conservation decisions.

In the case of conserving and managing grizzly bear populations, we believe it highly unlikely that an objective and scientific quantification of trends, whether from demographic parameters, mark–recapture studies, or other indices, will ever reduce the portion of the probability distribution overlapping 1.0 to less than the conventional 5%, regardless of the health of the population. There are only 2 ways probability of decline in this sense can be minimized: either the rate of increase must be so high that the lower confidence interval is >1.0, or the confidence interval itself must be narrowed. But even the most robust grizzly population can only achieve a relatively modest rate of population increase. Thus, even a very fast-growing grizzly population will not likely yield documentation capable of rejecting a statistically plausible claim that it had, in fact, declined. Grizzly bears are difficult and expensive to study, and they exist in low densities. Thus, obtaining sample sizes needed to narrow the confidence interval surrounding the point estimate of λ will be very difficult, and for small populations, mathematically impossible. Further, grizzly bear populations can only have positive rates of increase for a finite time; even if human constraints were removed, a bear population will eventually converge on a long-term, mean rate of $\lambda = 1.0$. In fact, this is the very goal of conservation. A population that increases consistently for more than a few years is below carrying capacity either because the habitat has changed or humans have killed too many. In the ideal world of healthy bear populations, all would, over a period of a decade or so, have $\lambda = 1$. But if true λ is 1.0 and sampling errors are symmetrical, then fully half the probability distribution must suggest a population decline.

Thus we see no escape from uncertainty. To claim that no decision about what has occurred should be adopted until uncertainty is removed, or to claim that the only acceptable decision adopts some lower confidence limit as truth, is to reject the role of science. If the possibility of population decline is treated as the fact of population decline (even where overwhelming evidence suggests otherwise), there is no need to spend money on research or monitoring because the management approach would be identical regardless of what data were produced. Because it is impossible to absolutely reject the hypothesis of decline, one would always manage as though a decline had occurred. To us this would seem poor policy.

Instead, we suggest that 3 slightly more refined principles should guide future management of the GYE grizzly bear population (as well, we suspect, as other grizzly bear populations facing similar conditions in the American west). First, regardless of their present population health, their legal status, or which governmental agency has primary jurisdiction, we believe that grizzly bears can never again be viewed as an ordinary species. Specific regulations and agency responsibilities may change, but grizzly bears require careful and adaptive management efforts. This is not to say that the most extreme measures are always needed. Rather, this recognizes that habitat for grizzlies in the U.S. has, for all we can tell, permanently contracted to where there will always be legitimate concern about their long-term viability. We are optimistic that, with continued vigilance, these populations can persist indefinitely. But normal management, in the sense we have grown to expect from our experience with ungulate or black bear populations in the western U.S. over the past few decades, is not a term we associate with grizzly bear conservation.

Our second principle is to distinguish between short-term (reversible) and long-term (irreversible) impacts to grizzly bear populations. We suggest that a very stringent approach should be taken toward the latter, while considerably more flexibility should be accorded to the former. Most impacts resulting in direct mortality, even to the adult female segment, belong to the short-term, reversible category. Certainly, grizzly bear populations respond more slowly to losses than most other managed species, but even they can recover from most declines. Some changes in habitat also are short-term and reversible; after all, before the 20th century, grizzlies adapted to environments that fluctuated with climate, fire and post-fire succession, and other such changes. By contrast, actions or developments that remove land as functional grizzly habitat tend to be permanent. These actions are a long-term threat to any grizzly population as hemmed-in by humans as the GYE population. It is here that our uncertainty about the future, notwithstanding the positive news of the past 2 decades, rises to a position of deference, and should appropriately make us manage conservatively.

Finally, we view managing under uncertainty as a more nuanced craft than a naïve application of the 'precautionary' approach. We will almost always have doubt about the true status of the population. This doubt can be reduced with monitoring, particularly by integrating information from several indices, but it cannot be completely extinguished. The scientist's job is straight forward: as objectively and transparently as possible, report the level of certainty of conclusions and attach appropriate statistical caveats. For professional managers, the task is tougher, because it requires admitting that any decision made may be wrong, and that it may produce unwanted damage to a resource or interest, or entail unanticipated costs. This requires courage because such an admission may cause managers to appear incompetent when they are merely being honest. It also requires managers to adapt and respond to conditions that are rarely if ever static.

For the interested public the task is perhaps toughest of all. We submit that more productive public involvement requires that citizens transcend focusing on their immediate concerns (e.g., risk to grizzly bear population viability, risk to economic interests) and acknowledge that benefits (perhaps accruing to others) accompany those risks. We don't advocate simplistic risk:benefit analyses when it comes to making decisions bearing on grizzly recovery, because any such analyses pre-suppose an agreed-upon set of values. Rather, we advocate acknowledging differences in values among various stakeholders while minimizing judgments about which values are superior.

Those who value healthy grizzly bear populations should acknowledge the legitimate costs that conservation imposes on other segments of society, and the fact that these costs increase as our willingness to accept risk declines. Those to whom grizzly bear recovery poses hardships should similarly accept that the burden of proof has historically been placed on the species rather than on us (i.e., demonstrating that an action causes harm rather than no harm), and that to manage risk of further declines or extirpation to a level of societal comfort, some lost opportunity or unfortunate costs will be inevitable. The long-term conservation of grizzlies in the GYE requires acceptance among various interest groups of both grizzly bears and of differing social values.

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